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ASPECTS OF RESOURCE PARTITIONING IN SOME CHAREMOPHILOUS HYMENOPTERA

by

© ROBERT W. LONGAIR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

DEPARTMENT OF ENTOMOLOGY

EDMONTON, ALBERTA

FALL, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ASPECTS OF RESOURCE PARTITIONING IN SOME CHAREMOPHILOUS HYMENOPTERA submitted by Robert W. Longair in partial fulfilment of the requirements for the degree of Master of Science in Insect Ecology.

W. G. Evans
Supervisor

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D. A. Craig

Date August 17, 1978

To Dr. A.S. West whose interest

and encouragement made this possible.

ABSTRACT

Artificial trap-nests were used to study a group of aculeate Hymenoptera which nest in holes in wood, with respect to resource partitioning theory. The species in this group show differences in diameter of holes selected for nesting, periods of nesting during the summer, and food selection. Such differences delimit a number of close associations within this guild, rather than all species being evenly "spaced" along the resource dimensions examined. While some species show distinct differences from others, most partitioning appears to be the result of small differences on a number of dimensions, rather than large differences over a single dimension.

Niche breadth and overlap measures and dendrograms drawn from these, indicate that narrow breadth (specialization) is associated with rare or uncommon species, while broad breadth is characteristic of abundant species. Implications to general ecological theory are considered in light of these findings.

Additionally, phenomena related to use of different hole diameters, i.e. parasitism and sex ratio of offspring are considered. Sex ratios of some species show variation with diameter, and with generation during the summer. Differential investment in males and females at different times may help reduce competition.

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Chapter 1 - Introduction

1.1 Resource Partitioning

Coexistence of groups of species within a community is dependent on the ability to reduce, or keep at a minimum level, competition for available resources. This differential use of various resource dimensions is known as resource partitioning. Schoener (1974) has stated that "the major purpose of resource-partitioning studies is to analyze the limits interspecific competition places on the number of species that can stably coexist". The inherent relationship between use of resources and competition is particularly evident in ecologically similar species, where high levels of competition may result in various phenomena, such as character displacement and ecological shifts, based on the competitive exclusion principle.

Fundamental to examination of differential resource use is the concept of the niche of a species, variously defined prior to Hutchinson's (1957) theoretical treatment of it as a multidimensional hypervolume, the dimensions being the various resource requirements involved, within which a species could survive. The fundamental niche of a species is defined largely on the basis of historical and genetic factors; thus limits to the niche available to a species, in the absence of competing species, is the result of a combination of physiological and behavioural restrictions within the population. The realized niche, the only "form" of the niche encountered in actual field studies on animals, is then the

restricted fundamental niche, limited by the actions of other elements in the community, and of primary importance to studies on competition and resource partitioning.

Within a community, units more closely related ecologically to one another than to members outside that unit may be discerned. Root (1967) has defined such units, or guilds, as a group of species that exploit the same class of environmental resources in a similar manner. Analysis of competition within a given guild would appear then to be more useful in examining resource partitioning than in a study of the community as a whole.

In the present study, I have examined a group of hole nesting aculeate Hymenoptera to determine the type and extent of resource partitioning along three major dimensions, those of nest hole size, seasonality of nest construction, and larval nutrition.

Previous works on resource partitioning are relatively numerous, though vertebrates, such as birds (Cody, 1974), reptiles (Pianka, 1973, 1975), and amphibians (Inger and Colwell, 1977) have been emphasized. These works are particularly useful in examining the theoretical and practical aspects of quantifying niche form and interaction, and Schoener (1974) has additionally reviewed many of the more recent works dealing with this topic.

The number of works on invertebrate groups is smaller; nevertheless, some excellent papers dealing with niche quantification and resource partitioning have appeared. Much work has dealt with parasitoid Hymenoptera, and this is important for understanding an ecological framework for introduction of agents of biological

control. Studies of major importance include those of Heatwole and Davis (1965) on differential host attack by sympatric species of the genus Megarhyssa, and Price (1970, 1971) on parasitoids of sawflies. In other hymenopterous groups, Brian (1957) and Heinrich (1976) examined resource partitioning in bumblebees foraging on flowers. Price (1974) cites numerous other examples of work on insect groups.

Various authors have defined the main dimensions usually involved in resource partitioning. Schoener (1974) recognizes three: food type, time and habitat (Pianka, 1975 describes these as trophic, temporal, and spatial separation). Many studies have concentrated on trophic partitioning, undoubtedly often the most important factor being partitioned, which is additionally sometimes more easily examined than the other factors.

The present study involves gaining some understanding of resource partitioning in an association of insects using at least one similar resource, nesting holes, by means of quantitative measures of certain niche dimensions. By so doing, a baseline for later intercommunity comparisons can be established, and relations between the species present can be discussed in light of ecological theory.

There is an obvious need for similar quantitative work dealing with various resource dimensions within guilds and communities, especially in invertebrate groups.

Additionally, I will discuss phenomena related to one of the

dimensions examined, hole size, including parasitism on some species and offspring sex ratio and the effect of hole size selection on these.

1.2 Charemophilous Hymenoptera

The association of species examined in this study have previously been known as trap-nesters. This is unfortunate, since the name is not based on intrinsic properties of the animals involved. Virtually any group could be defined as "trap-nesters" provided that the trap was adequately designed. The characteristic use of hollows and holes constructed by other agents suggests a useful term to designate this group of aculeate Hymenoptera. I have elected to use the term charemophilous (Greek; charemos - a cleft, cavity or hole and philos- loving).

Charemophilous Hymenoptera are wasp species whose adults use existing holes usually in a woody substrate, often abandoned beetle burrows. Into such a cavity a female brings provisions consisting either of prey, or pollen-nectar mixtures, to feed the larvae, which have been placed as eggs either before or after provisioning. A female then seals its cells with various materials (see below) forming either one or two walls between cells. Some omit such partitions. A final closing plug effectively separates females from offspring. Females then proceed on to construct various numbers of other similar nests.

Nesting in holes in wood is exhibited by a rather diverse assortment of Hymenoptera. Iwata (1976) recognizes two main types:

burrowing forms, and renting forms, the latter equivalent to the charemophilous group introduced above. Burrowers generally construct their own nests, removing the substrate to produce a hole, although many burrowers undoubtedly use existing cavities, as the renters do. In the burrowing group, by far the majority nest in pith or rotting wood; only the large carpenter bees, the Xylocopini, are strong enough to excavate nests in sound wood.

Based on diversity of forms displaying such behaviour, though often only distantly related phylogenetically, and the relative restriction of it to certain genera within families, it seems likely that wood nesting is a derived form of behaviour, evolved from ground nesting behaviour present in some representative species in each of the families. While such nesting habits are relatively rare in Sphecidae and Pompiloidea, groups like Eumenidae and particularly Megachilidae may be restricted almost entirely to use of such a nesting substrate. Figure 1 indicates the groups in which this type of behaviour is displayed among the aculeate Hymenoptera. This does not include groups such as some Formicidae, which while nesting in wood, exhibit truly social behaviour, unlike the primarily solitary Hymenoptera examined in this study.

The nature of convergence of this form of behaviour explains, to a large extent, some of the differences in materials used for provisioning, and partitioning, sequence of provisioning and other phenomena. As will be discussed, such differences are important in resource partitioning.

Materials used for construction of nests vary among different

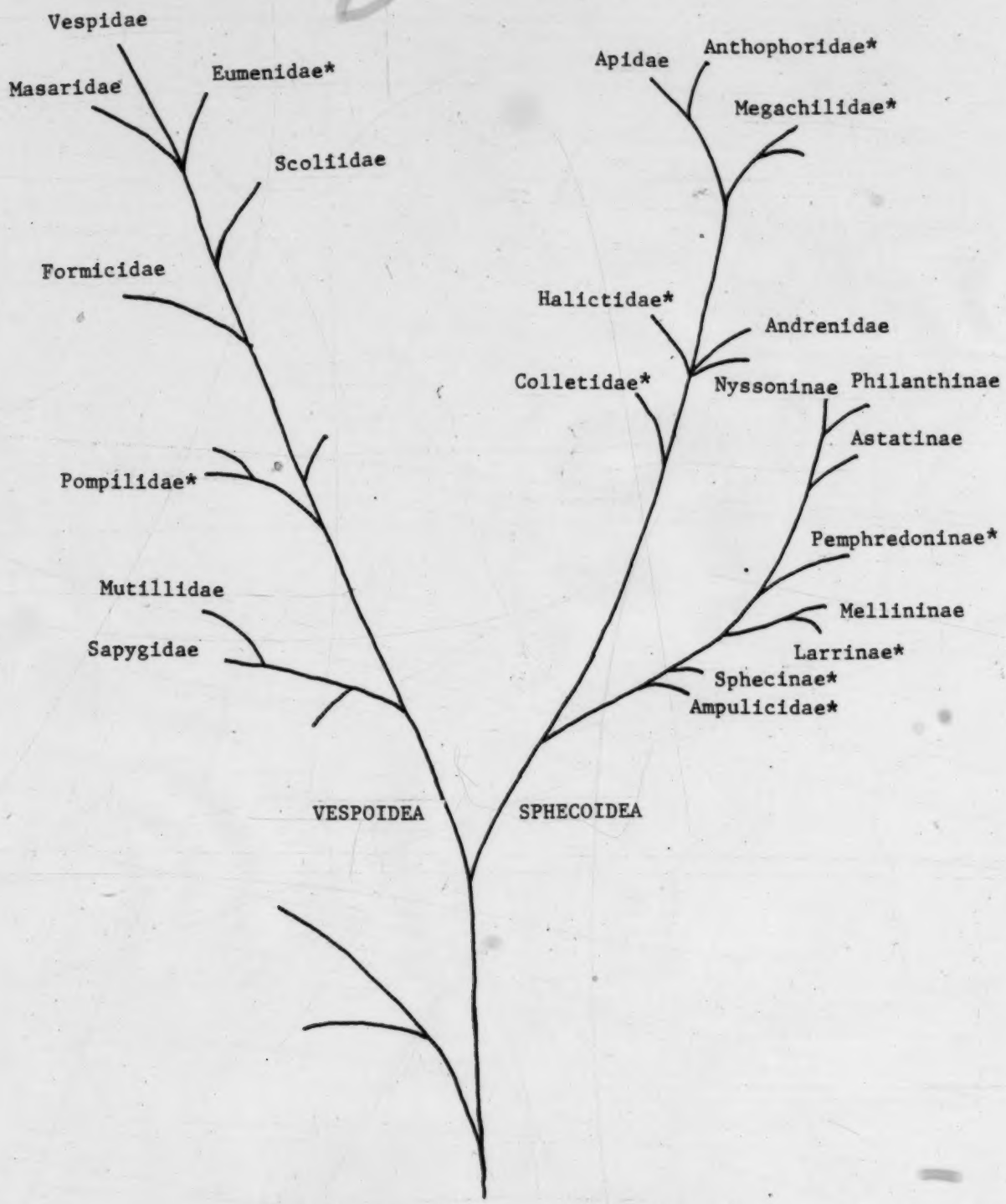

Figure 1 - Phylogeny of aculeate Hymenoptera (adapted from Brothers, 1975; Sphecoidea after Bohart and Menke, 1976) showing various taxa including those with representatives displaying charemophilous behaviour(*).

groups of Hymenoptera. Sphecid females make cell partitions and closures of wood or pith, debris, plant fibres, or mud. Eumenid females are remarkably inflexible in their behaviour, members of all groups partitioning and closing the nest with plastic materials, primarily mud. Megachilid females seem most specialized in this respect, for the most part using leaf pieces for cell construction and nest closure, though some members use resin instead.

By far the most extensive work published on charemophiles is Krombein's (1967) book, dealing with a large number of species from various parts of the United States. This work includes details of nest construction and dimensions, prey used, parasite species present, other biological data, and a review of earlier work. Similarly, a number of papers have been published on the Wisconsin fauna, primarily on a species by species basis (Medler, 1955, 1958, 1963, 1964a, 1964b, 1964c, 1964d, 1965, 1966a, 1966b, 1967a, 1967b; Koerber and Medler, 1958; Medler and Koerber, 1957; Medler and Fye, 1956). These again are largely observational, restricted to the species studied, with nests taken across the entire state, and which describe, as does Krombein (1967), nest features and prey data. Fye (1965a, 1965b) has examined these insects in northwestern Ontario. A discussion of much of the work on the behaviour of world fauna can be found in Iwata (1976).

As noted above, many of these studies have been devoted primarily to survey-type observational reports on wasps and bees, usually restricting any discussion of species interactions to records of supersedure. An exception is the work of Cooper (1953, 1957) on the nesting behaviour of Ancistrocerus antilope (Panzer), a

eumenid; this exemplary study is undoubtedly the most intensive examination of the behaviour of individuals involved in the nesting process. Such studies are few, however, and many aspects of the behaviour of charemophilous aculeates are inadequately understood and observed by few entomologists.

Study of these insects has reached a point where observations of the fauna give distribution records for many areas of North America. With large numbers of species cohabiting a given area, the opportunity for ecological studies of communities where these aculeates comprise a major part of the fauna should be examined more closely.

1.3 Present Study

The present work is an attempt to apply some of the theoretical ideas on resource partitioning to a guild of charemophilous wasps and bees taken from a single locality. While most of the species encountered here have been described and have had notes published on them, I am more concerned with interspecific interactions than with individual details of the life history of a given species. Previous work, particularly on prey data, is used although much of it is unsuitable for comparative purposes.

The noticeable presence or absence of elements of the charemophilous fauna in studies mentioned above indicates that each community examined will reveal some aspects of competition between associated groups. Comparative studies of geographically distant communities (Cody, 1974; Pianka, 1975) have proved useful in

studying practical aspects of theoretical community ecology. This is difficult without some form of quantitative analysis of the situations studied. In recent years, the use of mathematical niche measures such as niche breadth and overlap have allowed comparisons between communities. In this study, such measures are used; these clarify not only interactions within a community, but allow for comparisons with other areas which may be studied later.

Chapter 2 - Study Area

The field research was carried out at the Queen's University Biological Field Station at Lake Opinicon, near Chaffey's Locks in eastern Ontario, about 110 km (70 miles) south-southwest of Ottawa (44°33' N. 76°16' W.). The area is characterized by an underlying bedrock formation, part of the Canadian Shield, though areas somewhat further south are typically limestone, and the effect of this will be discussed below. Actual sites used were some kilometres from the main field station, and all were characterized by extensive secondary plant growth. At one site, two large fields, still cut yearly but unused otherwise, marked the centres of collecting areas.

Vegetation of the area is typical deciduous-coniferous forest, with an abundance of sugar maple, american elm, birches and poplar. As mentioned above, a portion of the surrounding area is devoted to farming, and both fields, and secondarily overgrown old fields are present. Such fields are invariably enclosed by relatively dense forest. Overgrown fields are typically characterized by low shrubs, milkweed plants, and the like, which form small dense clumps of vegetation throughout such areas. It has been noted (Harmsen, personal communication) that the biotic composition of the nearby limestone based area is unusual, and that some groups are present which on the basis of factors such as latitude might not be expected.

The proximity of this peculiar area to the study site may have an influence on the organisms present there. Thus, some of the species present may be at the extremes of distributional ranges. As discussed below, this may affect competitive ability and niche relations.

Chapter 3 - Materials and Methods

3.1 Previous Techniques

Use of artificially constructed nesting sites for aculeates has enhanced immensely the ability of researchers to study numerous aspects of the natural history of these insects. A number of different techniques have been used, with varying degrees of success. Cooper (1953) cites a number of earlier works using glass tubes imbedded in wood or paper. While ideally observation would be facilitated, high mortality often occurs due to excessive moisture levels allowing bacterial and mould infections. Cooper suggested the use of simple borings in easily split, straight-grained wood, a course which Krombein (1967) followed.

The other technique most commonly used has been constructing traps of natural objects, such as sumac pieces; this has been demonstrated by Medler (1955-1967) and various of his students, and by Danks (1970) in England. This method appears to be equally effective; Koerber and Medler (1958) obtained an occupancy rate of 47.2% in their study. Evans (1973) using both types of traps, had an occupancy rate of 61% for pine blocks, but only 6% for Sambucus stems.

Various other techniques have been investigated but appear to be relatively less successful. Medler and Fye (1956) used a domicile type trap with several holes bored in a number of pieces of connected board. Clay casts were also attempted (Fye, 1965a). Work with paper straws has been successful in attracting bees, but less so with wasps (Fye, 1965a). It appears the use of simple bored pine blocks

will encounter fewest problems. Variations on this theme have been tried (Krombein, 1970), to increase the ease of observation, including the use of clear plastic on one side of the trap. For behavioural studies, this method would seem most useful.

3.2 Present Study

Trap-nests were constructed of straight-grained white pine and cut from construction grade 2" X 4"'s. Krombein's (1967) success with this method, and Evans' (1973) lack of success with "natural" traps suggested that use of white pine blocks is more likely to be successful. In addition, the difficulty in obtaining sufficient sumac, and the ability to reuse white pine, ensured larger numbers of traps.

Blocks were cut to the dimensions 2.5 cm X 2.5 cm X 15 cm, allowing sufficient room for larger boring diameters, and long boring length. Holes were bored in one end of the block, to a depth of 90 mm - 100 mm, of five different diameters, 3 mm, 5 mm, 7 mm, 9 mm, and 11 mm. This range of sizes almost completely covers the range of hole diameters used by most groups of charemophilous wasps and bees. The necessity for adequate sample sizes for each hole size precluded use of a larger number of diameters.

Traps were bundled in groups of five, one of each hole diameter, and bound with wire, all open ends facing in the same direction; traps of a particular boring diameter were placed randomly within the bundle. By this means, an approaching wasp or bee had a complete choice of different hole sizes available to it. Each bundle was

numbered, and individual traps denoted by bundle number plus graded hole size (e.g. 134-3, 83-2).

In the field, bundles were attached to various substrates such as dead or live shrubs and tree limbs, with wire, to minimize movement in the wind, or placed on suitably solid objects, e.g. dead logs, tree stumps. Bundles were placed horizontally, with borings parallel to the ground. Locations of various bundles are shown in Figure 2.

Once a given trap was filled, it was immediately removed, although an attempt was made to avoid disruption of nest construction. Traps filled by occupants other than aculeates were also removed. Once a trap was removed it was replaced with an empty trap of the same size, and date of collection noted. During the summer, heavy rubber bands replaced the wire used to hold bundles together; this allowed more rapid replacement of filled traps, and provided they were checked and replaced when necessary, did the job adequately.

After examination of previous literature, and on the basis of first appearance dates of wasps and bees, it was decided to delay initial placement of traps until early June to avoid extensive use by other organisms (see below). Traps were set mostly between June 2 and June 16. This first setting consisted of 116 bundles (580 traps). At this time cursory checks of other traps were made, but they were not used until June 16. A second set of 39 bundles (195 traps) was added on June 30. The total number of traps set was 775; with replacements for filled traps, total presentation was 1120. Traps were checked every 2-5 days throughout June and July, while

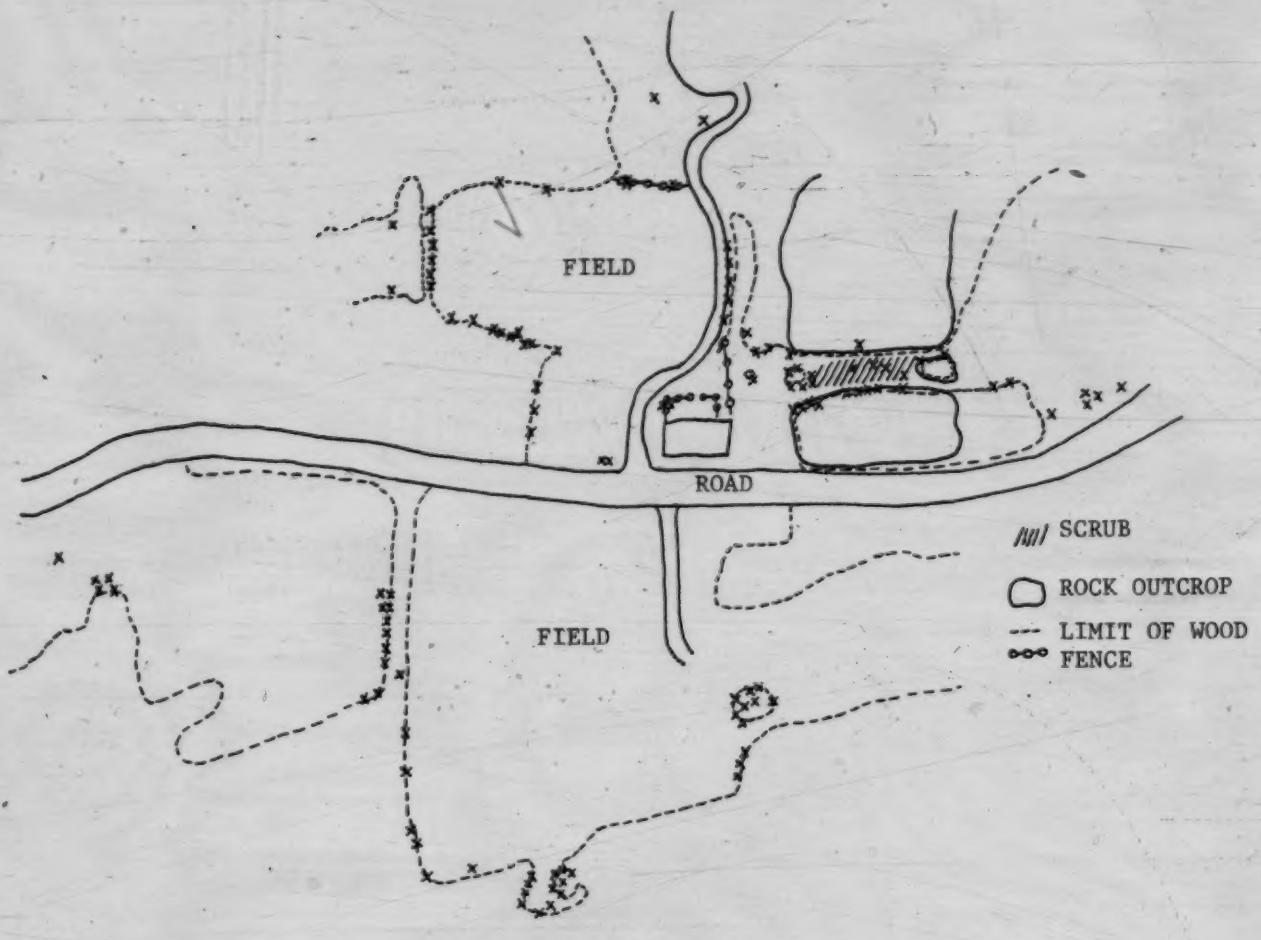

FIGURE 2 - LOCATION OF TRAP NEST BUNDLES (X) AT STUDY SITE AT LAKE OPINICON, ONTARIO

number of occupancies was high. When numbers of filled traps declined in late July and early August, collection was reduced to approximately once a week.

Occupied traps were split longitudinally to reveal nest contents. Details of nest construction, a large part of previous work, were not recorded, unless particularly unusual. Total number of cells, prey, and state of larvae were noted. Occupants of each cell were placed in individual vials, stoppered with cotton wool; each vial was labelled with a bundle, nest, and cell number. Prey specimens were removed from some nests and preserved in methyl hydrate for later identification. However, to guarantee sufficient emergence levels of adult wasps, this was only possible for a limited number of nests.

Emergent insects were killed with ethyl acetate and pinned for identification. Those which had not emerged by late September were placed, in their vials, in an incubator set at 2°C. After three months, larvae were removed from the incubator in three batches, to avoid simultaneous emergence. Each batch was exposed to increasingly long thermal shocks by exposure to 25°C. No defined light regime was used. Emergence rates were moderate to high. Larvae which died may have done so due to much lower humidity of rearing conditions than of their natural environment.

Chapter 4 - Charemophilous Hymenoptera

4.1 Results of Trap-nests

The rate of occupation achieved was comparable to that in other similar studies. Of a total presentation of 1120 traps, approximately 500 were used by aculeates, of which 451 survived for attempted rearing. The percentage of 44.6% is consistent with that expected and at least some material from 375 nests, or 83.2% of the possible total, was successfully reared.

Individuals of 17 species were reared from these trap-nests, belonging to four families of Hymenoptera: Eumenidae, Sphecidae (sensu Bohart and Menke, 1976), Pompilidae, and Megachilidae (this does not include parasites). Table 1 shows the identification and total number of nests for all species encountered. The relative abundance of different species varied widely from single nests for one leafcutter bee, and two eumenid species, to 91 nests for the commonest trap occupant, Megachile relativa, another leafcutter bee.

The species present differ markedly in a number of aspects of their natural history. Since prey type, hole size preference, and seasonality of nest construction are discussed below, I restrict descriptions here to brief details of nest construction, particularly materials used.

Table 1 - Aculeate Hymenoptera nesting in trap-nests and total number of nests for each species from Lake Opinicon, Ontario.

Taxon	Total number of nests
Vespoidea	
Eumenidae	
Ancistrocerus antilope (Panzer)	69
Ancistrocerus adiabatus (Saussure)	10
Parancistrocerus pensylvanicus (Saussure)	4
Euodynerus foraminatus (Saussure)	63
Symmorphus cristatus (Saussure)	13
unidentified Eumenidae sp. 1	1
unidentified Eumenidae sp. 2	1
Sphecoidea	
Sphecidae	
Isodontia mexicana (Saussure)	56
Trypargilum striatum (Provancher)	3
Trypoxylon frigidum Smith	5
Pompiloidea	
Pompilidae	
Dipogon sayi Banks	6
Apoidea	
Megachilidae	
Megachile relativa Cresson	91
Megachile mendica Cresson	28
Megachile inermis (Provancher)	10
Megachile pacifica Panzer	1
Megachile centuncularis (Linnaeus)	2
Heriades carinata Cresson	9
unidentified Megachilidae	2

4.2 Nesting Materials and Construction

4.2.1 Eumenidae

Females of all species of eumenids occupying traps use mud for partitioning and closure of the nest. Detailed accounts of nest architecture are reviewed and elaborated upon by Krombein (1967)

4.2.2 Sphecidae

Females of both Trypoxylon frigidum and Trypargilum striatum procure mud for nest construction. Females of I. mexicana were unique in using dried strands of plant material, primarily grasses, for nest partitioning. Several aspects of the nesting behaviour of this wasp species are worth noting. Closure of the nest is striking, with strands of many nests protruding up to 50 mm from the end of the boring. Temporary closure of the nest, during provisioning, is common. In addition, individuals of this species show a varied degree of nest partitioning, from total separation of each cell, to the presence of a single large brood chamber, where non-cannibalistic larvae feed communally on stored prey. At least one of the nests opened lacked partitions, despite the presence therein of four cocoons, an unusually high number for the individual nests examined.

4.2.3 Pompilidae

D. sayi females were least selective in material used for partitioning nests. General debris,in the form of bark pieces, silk, plant material and other matter was employed, making the nests easily discernible on opening.

4.2.4 Megachilidae

Of seven species of leafcutter bee, females of five used leaf pieces for cell construction and nest closure. Females of three predominant species showed variable cell construction. Those of M. relativa, the most common, were invariably untidy collections of leaves, which on handling separated easily from the rest of the cell. In contrast, cells of M. mendica were precisely constructed, each approximating the form of a cylinder; leaf pieces were much more constant in size. While such differences in cell construction were not studied in detail, it is very likely that they could be used for discerning the identity of the occupant; furthermore, examination of leaf types used by different species could prove very worthwhile. Those used by M. relativa were hairy, tooth-edged types quite distinct from the bare, straight-edged leaves of M. mendica. It appears that the individuals of the third species, M. inermis, the largest leafcutters, also used a different leaf form, and displayed much sturdier cell construction.

4.3 Parasites and Nest Associates

Rate of parasitism was extremely low for most nests, probably due in part to their removal from the field soon after construction, eliminating attack by parasites which pierce the closing plug and oviposit in the nest. Detailed results were kept only for Chrysis coerulans F., the most common parasite in eumenid nests. These appeared commonly in nests of both abundant species of eumenid, and are discussed further below.

Other parasites were far less numerous. A single unidentified ichneumonid wasp was taken from one eumenid nest, as were a number of dipterous larvae and adults (possibly the miltogrammine Amobia). These flies usually destroyed a large part of any nest in which they occurred, moving from cell to cell by breaking down partitions, and consuming both wasp larvae and prey contents of cells. Small flies (Phoridae?) occurred as inquilines in some nests and psocopterans were often present as well.

The parasite fauna of leafcutter bee nests was quite distinct from that of Eumenidae. Two nests were parasitized by bombyliid flies (Anthrax sp.?) and larvae and adults of the ubiquitous eulophid parasite, Melittobia chalybii were present in several nests. A single nest revealed leucospidid parasites (Hymenoptera: Chalcidoidea). The most common nest parasites of leafcutter bees were individuals of Coelioxys sp. (Megachilidae). These occurred in several nests.

Except for fly parasites in eumenid nests, occupants of nests were rarely all destroyed, usually only a few cells within a given nest being damaged. If cells were parasitized, the total cell number in the nest was often small. This may have been a response by the provisioning wasp resulting in premature closure and abandonment of the nest. Detection of parasites by the host female may elicit such behaviour, and this is selected for where cleptoparasites oviposit in a sequence of cells in a single nest.

C. coerulans was the only important nest parasite on eumenids, infesting 48 of 153 nests provisioned by A. antilope or E. foraminatus, or 31.4% of the nests. Table 2 gives relative occurrence of parasites in nests of these two eumenid species; it would appear that

Table 2 - Nest parasitism by Chrysis coerulans on two eumenid species from trap-nests at Lake Opinicon, Ontario.

Nest hole diameter (mm)	Number of Euodynerus foraminatus nests parasitized	Number of Ancistrocerus antilope nests parasitized	Total number of nests parasitized*
5	2	1	11
7	5	9	24
9	3	3	9
11	2	2	4

parasitism is indiscriminate, its frequency being closely related to frequency of occurrence of the two host species. With rearing, there were never more than two parasitized cells per nest, and usually only a single cell (9 with 2, 39 with 1). This may merely emphasize the tendency of females to abandon parasitized nests. As I show below, the mean of the frequency distribution for this parasite in different hole sizes is exactly the same as that for E. foraminatus. In fact, the frequency distribution is more similar for these two species than for C. coerulans and A. antilope.

Coelioxys sp. parasitized 8.8% of M. relativa nests; unlike C. coerulans, these nests tended to have more parasitized cells. Of the eight nests, four had a single parasite, two had two, and two had three cells parasitized.

4.4 Other Organisms in Trap-nests

A number of other organisms tended to use borings for resting areas. The most common of these were small spiders which spun a sheet-like web across part of the opening, and various lepidopteran larvae which used the holes as pupation sites. One hole was used as a nesting site for a colony of ants, and in another an overwintering dealate queen ant was found. A few earwigs were found, using the borings as shelter during moulting periods. On the whole, such occupants were in very low numbers and presented little problem to occupation by wasps and bees. This source of competition for nesting sites may, at times of outbreaks of these competitors, be important. Here, however, numbers of non-aculeate competitors did not prevent charemophilous Hymenoptera from discovering suitable nesting holes.

4.5 Possible Competition from Other Hymenoptera

Organisms are not entirely free from competition outside a given unit like a guild. While competition is undoubtedly greatest between those species sharing a number of similar resources, other groups may impinge on resource use in less striking ways.

The study site supported several areas ideal for ground nesting wasps and bees, and these insects were frequently common. Possibly, some of these play an important role particularly with respect to food, in the association of charemophiles, since while not competing for nest sites, individuals of related species hunt similar prey, potentially excluding species which might otherwise exist within the guild examined. In addition, domestic honeybees were numerous at all times, and may have influenced location of nests, and food type of leafcutter bees.

Evans (1970, 1973) discusses a similar situation in a community of wasps, and the possible interactions between ground and hole nesting species. Under certain circumstances, these may be very important.

It is necessary to recognize that while examination of a group of obviously ecologically similar species may provide information on resource partitioning, it is rarely possible to determine all factors affecting a given group.

Chapter 5 - Nest Diameter Selection

5.1 Presentation of Nests

Traps of five different hole diameters were presented in a bundle. This allowed an approaching female, searching for a suitable hole, to select between hole sizes. Females, having been attracted to a location by appropriate vegetational cues, landed on bundles; it is unclear whether orientation to the bundles is originally based on visual perception of holes, or of the distinctive bundle. Natural nesting sites lack the distinctive buff colouration of artificial bundles, and it is possible that more searching for natural holes occurs on foot, than when artificial bundles were presented. Females may initially orient visually to any wooden substrate by profile or some such feature, and from a shorter distance to actual holes. Once a female has discovered a bundle, she proceeds to slowly investigate the entire wood surface for holes; on finding one, she enters, remaining in some holes for an extended period of time, emerges and usually continues searching. Even when the hole finally accepted is the one originally examined, a female usually enters at least two, and sometimes three other holes in a given bundle. There seems little doubt that the female is actively searching for more than just suitable nests, and is instead attempting to find the optimum nest size of the holes available.

Once the nest has been started, the female returns with unerring accuracy to the hole that she has chosen, despite the presence of

other holes of similar shape. This may be due to orientation to the location of the selected hole in relation to others in the bundle.

The range of diameters chosen for borings encompassed almost entirely those used by wasps and bees likely to occur in the area, as judged by previous works. It is possible that the full range of diameters acceptable to hunting females of some species was not covered, particularly at the large end of the scale. Nevertheless, for most species, the range of sizes allowed a complete choice of acceptable hole sizes for females.

Certain problems are inherent in such an experimental situation. An individual wasp or bee, completing a nest in a given bundle, is likely to examine and accept other diameters in the same bundle, within limits, rather than expend unnecessary energy searching out an entirely new bundle to find a "more perfect" hole. Of course, the choice will still be limited by the total acceptable size range. Multiple hole use within a bundle by one female did occur, though more frequently only single nests in a given bundle were constructed. Similarly, where one hole in a bundle has been filled, a searching female is faced with a restricted choice, though again her selection will reflect an acceptable range.

By replacing traps when filled, much of this problem was circumvented, but it was impossible to ensure that all nests were entirely clear all the time. In fact, replacement may make any niche dimension measure reflect a closer approximation to the fundamental niche, than the realized niche. Nevertheless, any such measurement reflects range and preference of hole size selection by species.

Some females interact directly, especially when a searching insect enters a hole where another is in the process of building. There does not appear to be any inhibition to nesting in a bundle with another female, either of the same or of a different species. The phenomenon of supersedure, whereby one female builds a cell in a nest already being constructed, indicates that most will take advantage of any available hole. In this study, supersedure was relatively rare.

5.2 Results

Table 3 shows distribution of nests in borings of different sizes, and mean and standard deviation of the frequency distribution for each species with five or more nests collected; means and distributions for hole selection were compared using Duncan's new multiple range test, and the results are included in Table 3. Figure 3 indicates the percentage of a given species occurring in each hole size. This figure shows the change in hole selection for different species across the range of diameters offered. Results of Duncan's indicate four distinct groups of means, with only one species, D. sayi, included in two groups. Three groups consist of few species, the largest hole size users, and separate groups of small hole size users. In contrast, the group using intermediate hole sizes includes almost half the species examined.

Clustering of these groups shows a lack of regular spacing along the resource gradient, as might be expected if the maximum number of species possible were present. Such clustering reflects

Table 3 - Distribution of charemophilous Hymenoptera in five diameters of holes in trap-nests from Lake Opinicon, Ontario, mean of frequency distribution and grouping of means by use of Duncan's new multiple range test.

Taxon	Hole diameters (mm)					Mean of frequency distribution	S.D.
	3	5	7	9	11		
T. frigidum	4	1	0	0	0	3.4	0.9
H. carinata	6	3	0	0	0	3.7	1.0
A. adiabatus	4	6	0	0	0	4.2	1.0
S. cristatus	0	8	4	1	0	5.92	1.32
D. sayi	0	1	5	0	0	6.7	0.8
C. coerulans	0	11	24	9	4	7.25	1.73
E. foraminatus	0	16	27	15	5	7.29	1.79
M. relativa	0	9	57	21	4	7.44	1.36
Coelioxys sp.	0	0	6	2	0	7.5	0.9
A. antilope	0	7	26	28	8	8.07	1.67
M. mendica	0	1	15	7	5	8.14	1.67
I. mexicana	0	1	7	26	22	9.46	1.48
M. inermis	0	0	0	5	5	10.0	1.1
Total	14	53	141	103	49		

Lines to right of means indicate results of Duncan's test; all means connected by the same line are not significantly different at the 95% level.

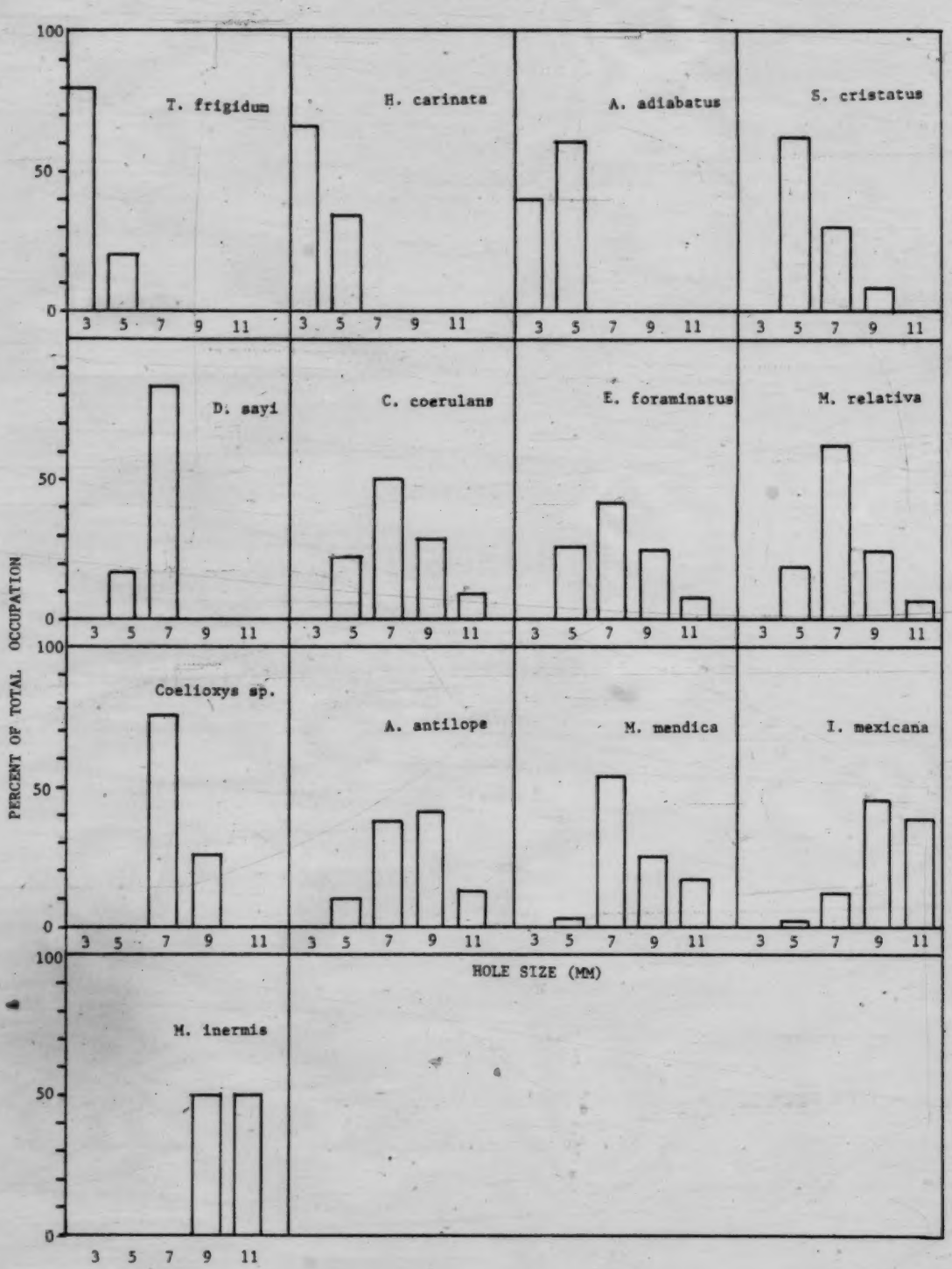

FIGURE 3 - PERCENT HOLE OCCUPANCY IN FIVE HOLE DIAMETERS FOR 13 SPECIES OF CHAREMOPHILOUS HYMENOPTERA FROM TRAP NESTS AT LAKE OPINICON, ONTARIO

on the idea of limiting similarity - how similar can individuals of associated species be and still coexist? This will be discussed later. With a small number of exceptions, species differ by at least 0.3 mm in mean hole selection, and the average difference in hole size for all these species is 0.85 mm. Two noticeable gaps in mean hole size used are between 4.2 mm and 5.9 mm, and between 8.1 mm and 9.5 mm. These discontinuities are supported by significant differences between groups of means. Such gaps contrast with the distinct clustering of some groups of species, such that a constant difference in mean hole size selected is not present as might be expected with maximum competition. For example, A. antilope and M. mendica have almost identical means for hole size selected, as do M. relativa, E. foraminatus, and C. coerulans. Similarities in hole size use, and potential competition for that resource may be circumvented by different times of use. This will be discussed in the following chapter.

5.3 Niche Breadth for Hole Size Selection

5.3.1 Niche Breadth Measure

Measurement of niche breadth allows an evaluation of the number of different resource states used for a given resource by a species, and the proportion of use for each resource state. Two measures of niche breadth, B, have been proposed (Levins, 1968):

$$\log B = -\Sigma p_i \log p_i \qquad \text{and} \qquad B = 1/\Sigma p_i^2$$

where p_i is the proportion of a species using the ith resource state of a given resource. Levins claims that there is no strong reason to prefer either measure; the latter has been used more frequently, especially in quantitative entomological studies (Price, 1971, 1974; Richards, 1978; also Pianka, 1973, 1974, 1975; Hespenheide, 1975) and appears to be accepted as adequate for such studies as the present one.

5.3.2 Results

Niche breadths for hole size selection for all species with more than five nests collected were calculated. Table 4 gives niche breadth values for these species, standardized for comparison with other resource measures by dividing by 5, the number of resource states. In addition, rank of each species with respect to both abundance and niche breadth is given.

Calculation of a mean niche breadth for all species allows discussion of species as specialists or generalists, depending on whether the niche breadth of that species is respectively less or greater than the mean for all species. While this technique is coarse, it does allow some comparison between species, and is appropriate here, since specialist/generalist comparisons are relative at any time.

In hole size selection, 4 of the 5 most abundant species are relative generalists, with niche breadths greater than the mean. On the other hand, less common species are either close to the mean, or less than it, and are described as relative specialists. An

Table 4 - Niche breadth values, breadth rank, and abundance rank for hole diameter selection in charemophilous aculeates nesting in trap-nests at Lake Opinicon, Ontario.

Taxon	Breadth value (B)	Breadth rank (descending)	Abundance rank (descending)
Dipogon sayi	.28	10	9
Trypoxylon frigidum	.29	9	10
Heriades carinata	.37	8	8
Ancistrocerus adiabatus	.38	7	7
Megachile inermis	.40	6	7
Symmorphus cristatus	.42	5	6
Megachile relativa	.44	4	1
Isodontia mexicana	.52	3	4
Megachile mendica	.52	3	5
Ancistrocerus antilope	.61	2	2
Euodynerus foraminatus	.64	1	3
Maximum breadth value	1.0		
Mean breadth value	.443		

exception to this is the most common occupant of the trap-nests, M. relativa, which has a niche breadth very close to the mean. This figure also verifies that niche breadth measures are affected by actual specialization or generalization of the organisms, rather than solely by number of samples.

5.4 Niche Overlap for Hole Size Selection

5.4.1 Niche Overlap Measure

This measure, which quantifies the extent to which two species use common resource states of a given resource dimension, follows Pianka's (1973) refinement of Levins' (1968) original formulae. The latter provided a different overlap value for the effect of species A acting on species B, than for species B acting on species A, dependent on niche breadths of the respective species. Pianka (1973) has used a symmetrical version of this overlap value such that the measure can range from zero to one. May (1975) has discussed the justification for such a symmetrical measure. Pianka's (1973) formula for overlap, O, is :

$$O_{j,k} = O_{k,j} = \frac{\Sigma p_{i,j} p_{i,k}}{(\Sigma p_{i,j}^2 \Sigma p_{i,k}^2)^{\frac{1}{2}}}$$

where $p_{i,j}$ and $p_{i,k}$ are the proportions of species j and k respectively in resource state i. Table 5 shows the matrix of overlap values for 11 most abundant apecies nesting in the traps.

As might be expected, those species with wide niche breadths have the largest mean overlaps. The least abundant groups have the

Table 5 - Matrix of overlap values for 11 species of charemophilous Hymenoptera from trap-nests at Lake Opinicon, Ontario.

Taxon	Taxon										
	1	2	3	4	5	6	7	8	9	10	11
1. *T. frigidum*	1.0	.99	.94	.22	.05	.11	.04	.04	.01	.01	0
2. *H. carinata*		1.0	.87	.40	.09	.21	.07	.08	.03	.01	0
3. *A. adiabatus*			1.0	.74	.16	.38	.12	.15	.05	.02	0
4. *S. cristatus*				1.0	.61	.79	.58	.54	.48	.20	.08
5. *D. sayi*					1.0	.84	.94	.68	.86	.20	0
6. *E. foraminatus*						1.0	.93	.91	.91	.58	.40
7. *M. relativa*							1.0	.89	.97	.48	.29
8. *A. antilope*								1.0	.92	.79	.64
9. *M. mendica*									1.0	.66	.49
10. *I. mexicana*										1.0	.98
11. *M. inermis*											1.0
Mean overlap	.24	.28	.34	.46	.44	.61	.53	.56	.54	.30	.29

Grand mean = .426

smallest mean niche overlaps, a fact which might initially be expected to indicate less competition, and potential for increased numbers. Each of these species, however, has at least one other species with which it shows extensive overlap.

Cody (1974) has developed a technique for schematic representation of grouping of guild members with highest overlap. This takes the form of a dendrogram based on a revised community matrix, the derivation of which Cody describes. Essentially, two species with the highest overlap are combined to form a new unit, and new overlaps with the rest of the matrix are calculated, based on the formula that the new overlap of the new unit with each remaining species is equal to the average overlap of each of those remaining species with the new combined species. Thus

$$O_{c,\,new} = \frac{O_{c,a} + O_{c,b}}{2}$$

where $O_{c,a}$ and $O_{c,b}$ are the overlap values between species c and a, and c and b respectively, $O_{c,new}$ is the overlap value between species c and unit "new", and "new" is the unit formed by the combination of species a and species b. The resulting dendrogram can be seen in Figure 4, where groups are connected at a given overlap level. On examination, it becomes apparent that the species are clustered in three relatively distinct groups, which might simplistically be called small, medium, and large hole size nesters. Note that the groupings are very similar to those distinguished by the use of Duncan's test, in the earlier part of this chapter. In each of these groups, at least two species show extensive overlap.

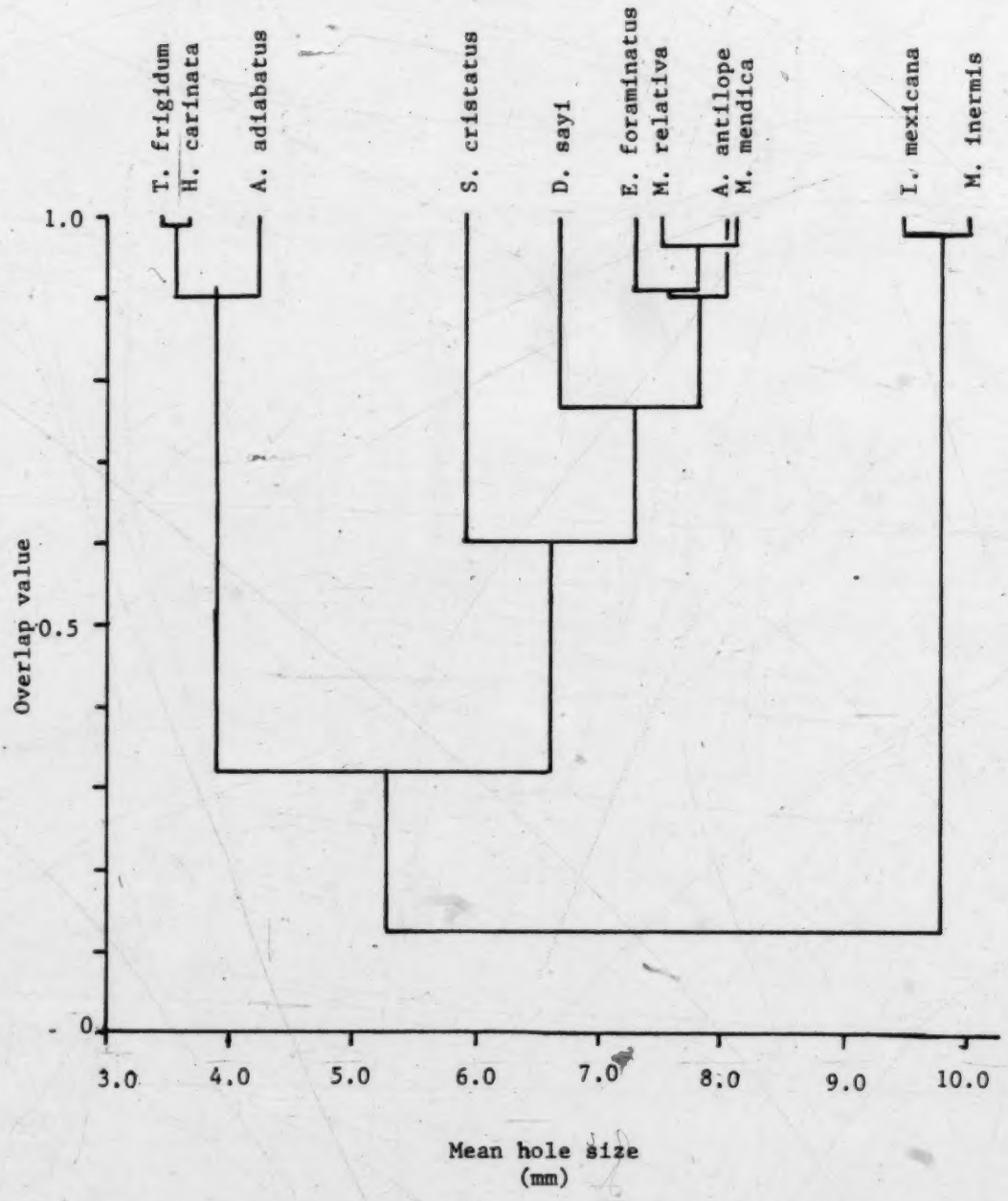

Figure 4 - Dendrogram showing grouping by overlap values for hole size selection in 11 species of charemophilous Hymenoptera from trap-nests at Lake Opinicon, Ontario

However, both "large" and "small" groups consist of only two or three species, and are quite separate from the core of species nesting in medium hole diameters. The group including six species tends to use such medium hole sizes. Of these six, the four most abundant all display a high degree of overlap, while D. sayi and particularly S. cristatus, are somewhat more isolated.

It can be concluded that while almost all hole sizes are used to some extent, a number of species are concentrated in a central core of intermediate hole size, and these are four of the most abundant species, displaying much higher than average overlap.

Chapter 6 - Nest Construction Phenology

6.1 Introduction

Records for dates are based on periodic checks of traps during the summer. These dates are discussed in "Materials and Methods". For purposes of analysis, collection dates were aggregated in seven day blocks to reflect population changes rather than differences in the number of traps examined on a given day.

Difficulties arise in determination of precise dates of nest construction. For most nests, if any sign of construction was apparent on examination, that particular date is designated the collection date. As such, dates recorded are within two to three days of construction time. For determining numbers of nests for comparative purposes I standardized the number of traps available for occupation. Prior to June 30, 580 traps were available; after this date an additional 195 were added. Thus all numbers of nests before this date have been increased by a factor of 1.34. This results at most in an increase of only one or two nests for the species involved.

6.2 Results

The overall number of nests per collection period reflects a bimodal distribution of frequency of trap use with a distinct decrease in numbers in late July and early August, and is likely the result of bivoltinism in most of the more abundant species encountered. Figure 5 shows this bimodal distribution.

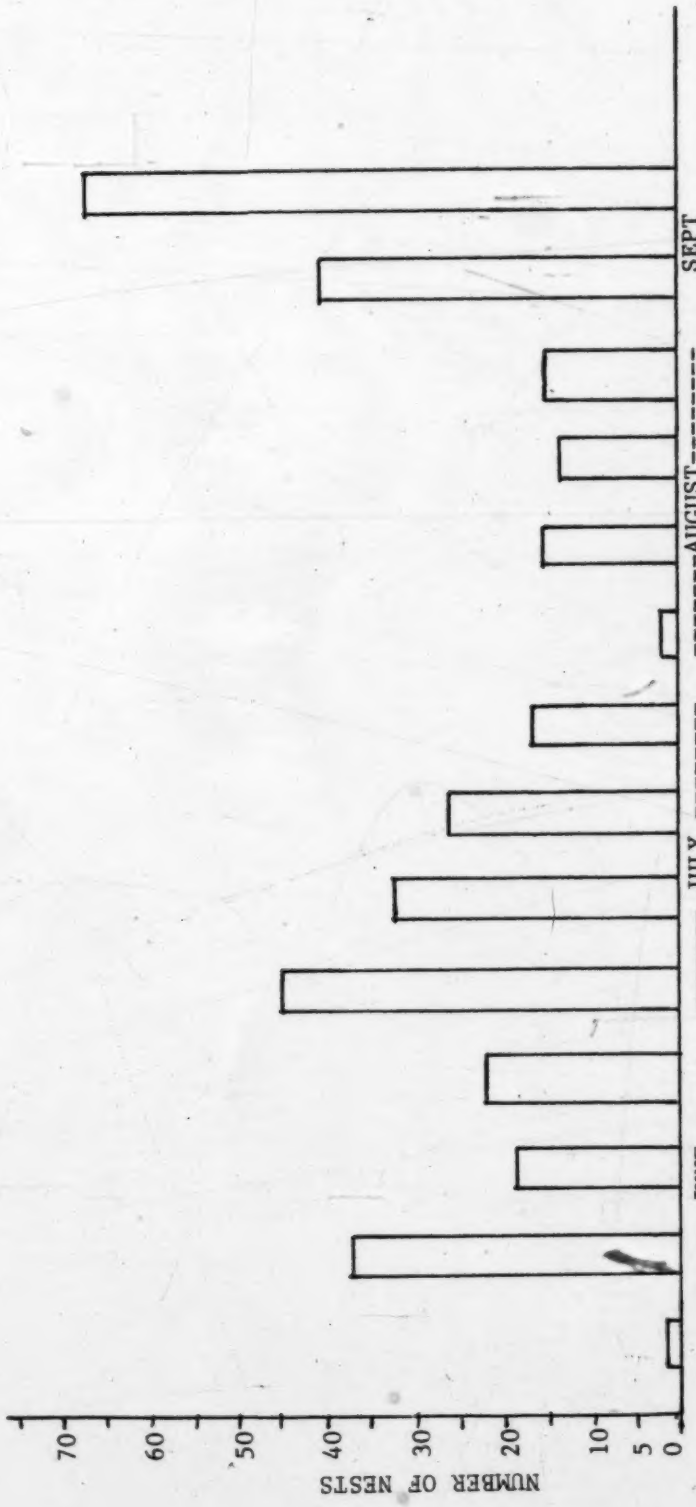

Figure 5 - Frequency distribution of trap-nest occupation during the summer at Lake Opinicon, Ontario by charemophilous Hymenoptera

However, a number of species appear to be univoltine. These latter include S. cristatus, I. mexicana and two species, A. adiabatus and P. pensylvanicus, which appeared only as a summer generation, but must have some individuals which overwinter, though these were not collected. Another possibility is that adults overwinter, but this seems unlikely in view of the characteristic eumenid pattern of overwintering as larvae.

In some of the abundant species, numbers increased markedly at the end of the summer. A subsequent drop is not in evidence due to the necessity of terminating collection by the middle of September, but the pattern coincides with that found by Michener (1954) working with Megachile brevis, and a precipitous decline can be assumed. Figure 6 shows the frequency distribution throughout the summer for nine species. Each point is plotted as a percentage of maximum number of nests for that species in any one seven-day period during the summer

These figures illustrate a number of factors involved in differential nesting periods. For example, the two most common eumenids, while both displaying bimodal frequency distributions, differ in the peak of these periods. E. foraminatus occurs earlier than the related A. antilope. Similarly, in examining three common species of leafcutter bees, M. relativa occurs first, earlier than either M. mendica or M. inermis, while the peak frequency for the latter occurs when both other species are absent from the traps.

Certain groups, like S. cristatus, show a single peak early in the summer.

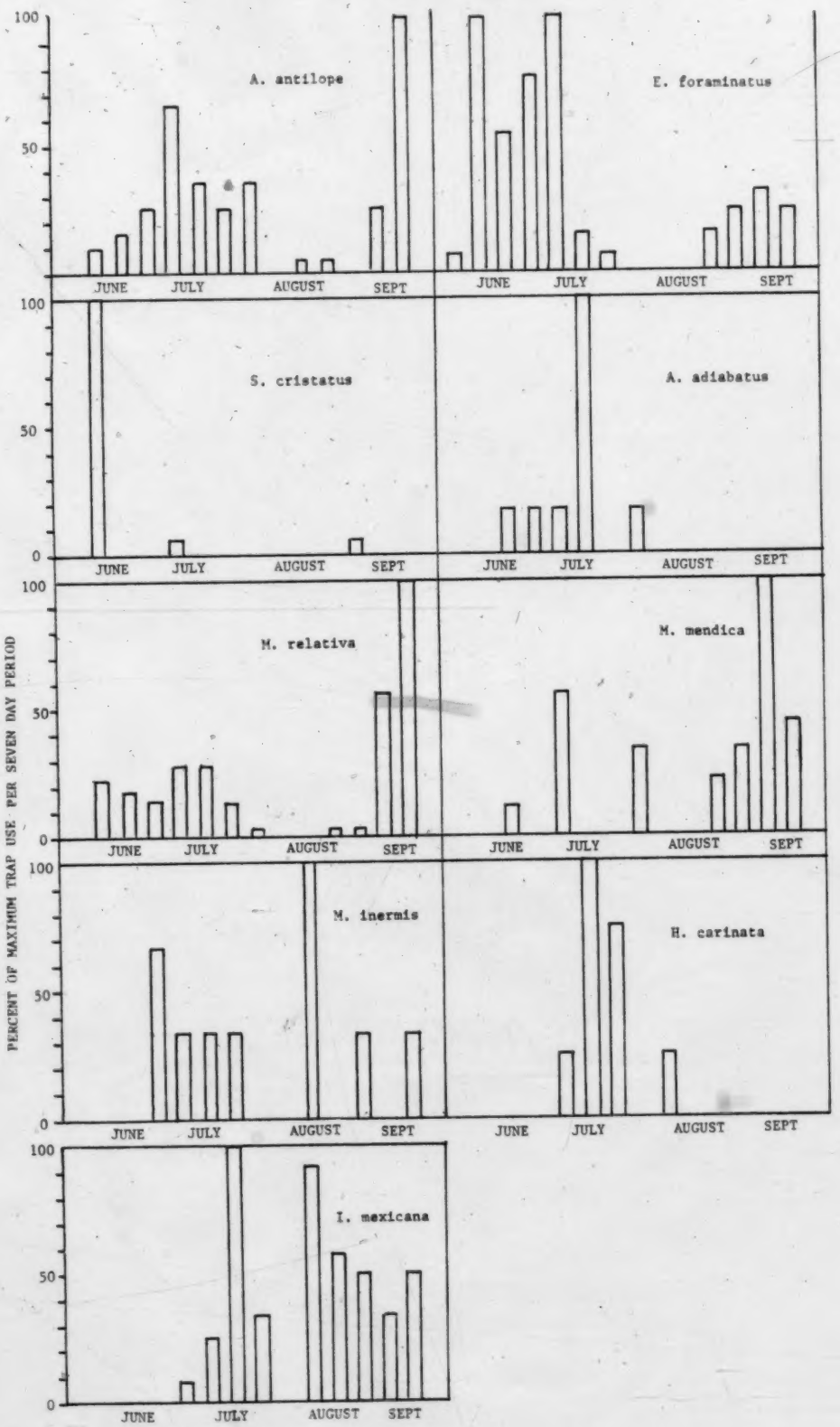

FIGURE 6 - SEASONAL DISTRIBUTION OF NEST CONSTRUCTION AS PERCENTAGE OF MAXIMUM NESTS PER SEVEN DAY PERIOD FOR 9 SPECIES OF CHAREMOPHILOUS HYMENOPTERA FROM TRAP NESTS AT LAKE OPINICON, ONTARIO

I. mexicana most clearly illustrates differences in flight and nesting period. Nest construction by individuals of this species does not commence until mid-July and peak nesting frequency occurs during the decline of most other species.

Factors involved in seasonality of nest construction are undoubtedly closely related to availability of resources. For I. mexicana, prey availability also probably plays a role; certainly the unusual habit of using dry grasses for nesting material means that a mid-summer nesting period would coincide with the ripening and drying of such plants. Numbers of beetle borings will change during the summer as well, and timing of nest construction may coincide with peaks in such hole availability.

However, the differences between groups such as E. foraminatus and A. antilope cannot be explained by prey availability or nesting materials, since these resources are available throughout the summer. Whether this is an adaptation to some unmonitored resource or a case of an ecological shift to avoid competition is unclear.

6.3 Niche Breadth for Nest Construction Phenology

Niche breadths for nest construction phenology were calculated as for hole size and standardized by division by 14, the number of resource states. Table 6 gives measures for nine species for which sufficient collection records allowed meaningful calculation. It must be recalled that such figures may be based on either a bimodal or unimodal frequency distribution; this would mean that a single broad peak in frequency could produce a breadth measure equal to

Table 6 - Niche breadth values, breadth rank, and abundance rank for nest construction phenology in charemophilous aculeates from trap-nests at Lake Opinicon, Ontario.

Taxon	Breadth value (B)	Breadth rank (descending)	Abundance rank (descending)
Symmorphus cristatus	.09	9	6
Ancistrocerus adiabatus	.18	8	7
Heriades carinata	.22	7	8
Megachile mendica	.36	6	5
Megachile relativa	.37	5	1
Megachile inermis	.40	4	7
Ancistrocerus antilope	.46	3	2
Euodynerus foraminatus	.48	2	3
Isodontia mexicana	.49	1	4
Maximum breadth value	1.0		
Mean breadth value	.34		

that produced by a pair of narrower peaks. The two common eumenids, E. foraminatus and A. antilope, show very similar breadths, as do M. relativa, M. mendica, and M. inermis, the three leafcutter bee species. On the other hand, single generation species with small numbers of nests display relatively narrow niche breadth. I. mexicana, the other univoltine species, differs in that it has the largest niche breadth of all species examined, for nest construction phenology. The broad nature of the seasonality of this species may be due to lack of abundant competitors for prey and hole size. Whether a "seasonal specialist" like S. cristatus is limited by prey availbility is difficult to determine, although this appears possible. This species occurs in relatively large numbers before any other group, and is then virtually absent for the rest of the summer.

For nest construction phenology, it is more difficult to compare specialists and generalists, using the mean for niche breadth as a comparative point, since the narrow breadth measure for S. cristatus reduces the mean considerably. Note, however, that no species is extremely broad niched (generalized) with respect to nesting period. In comparison, some extreme specialists do occur, as mentioned above. The overall reduced niche breadths are undoubtedly due in part to either small numbers of individuals, meaning that they appear in only a few resource states, or to the bimodal distribution.

6.4 Niche Overlap for Nest Construction Phenology

Overlap is calculated as above for hole size distribution, and Table 7 shows the matrix for overlap values for nest construction phenology. A large portion of the species examined show moderate mean overlap with other species, and overlap between any two species is rarely greater than 0.8. Only one species, S. cristatus, is isolated in a seasonal enclave position, appearing much sooner than other species. This, at first sight, appears contrary to what might be expected. A species separated from its nearest "ecological neighbour" would seem capable of taking advantage of unused niche space, perhaps by expansion to include somewhat later dates. However, any shift in nesting period for S. cristatus might be precluded by a number of factors. If prey is restricted in seasonal appearance, little flexibility is possible, since as will be seen later, this species is highly specific in prey choice. In addition, any shift to a later date might cause more severe overlap with the earlier occurring, abundant E. foraminatus.

Figure 7 shows the dendrogram calculated from the overlap matrix for seasonality of nest construction. As mentioned above, few pairs show extreme overlap, and the highest overlaps produce essentially four groups: one of M. inermis and I. mexicana, one of H. carinata and A. adiabatus, one of S. cristatus and E. foraminatus, and one of M. mendica, M. relativa, and A. antilope.

These correspond approximately to a late, single peak group, a mid-summer, single peak group, an early group, and a two peak full summer group.

Table 7 - Matrix of overlap values for nest construction phenology for 9 species of charemophilous Hymenoptera from trap-nests at Lake Opinicon, Ontario.

Taxon	Taxon								
	1	2	3	4	5	6	7	8	9
1. *S. cristatus*	1.0	.61	.01	.01	.03	.10	.04	.19	.20
2. *E. foraminatus*		1.0	.20	.29	.43	.58	.48	.52	.21
3. *H. carinata*			1.0	.76	.36	.39	.08	.27	.46
4. *A. adiabatus*				1.0	.34	.40	.12	.29	.18
5. *M. inermis*					1.0	.50	.24	.37	.70
6. *A. antilope*						1.0	.65	.89	.49
7. *M. mendica*							1.0	.72	.44
8. *M. relativa*								1.0	.44
9. *I. mexicana*									1.0
Mean overlap	.13	.41	.32	.30	.37	.50	.35	.46	.37

Grand mean = .361

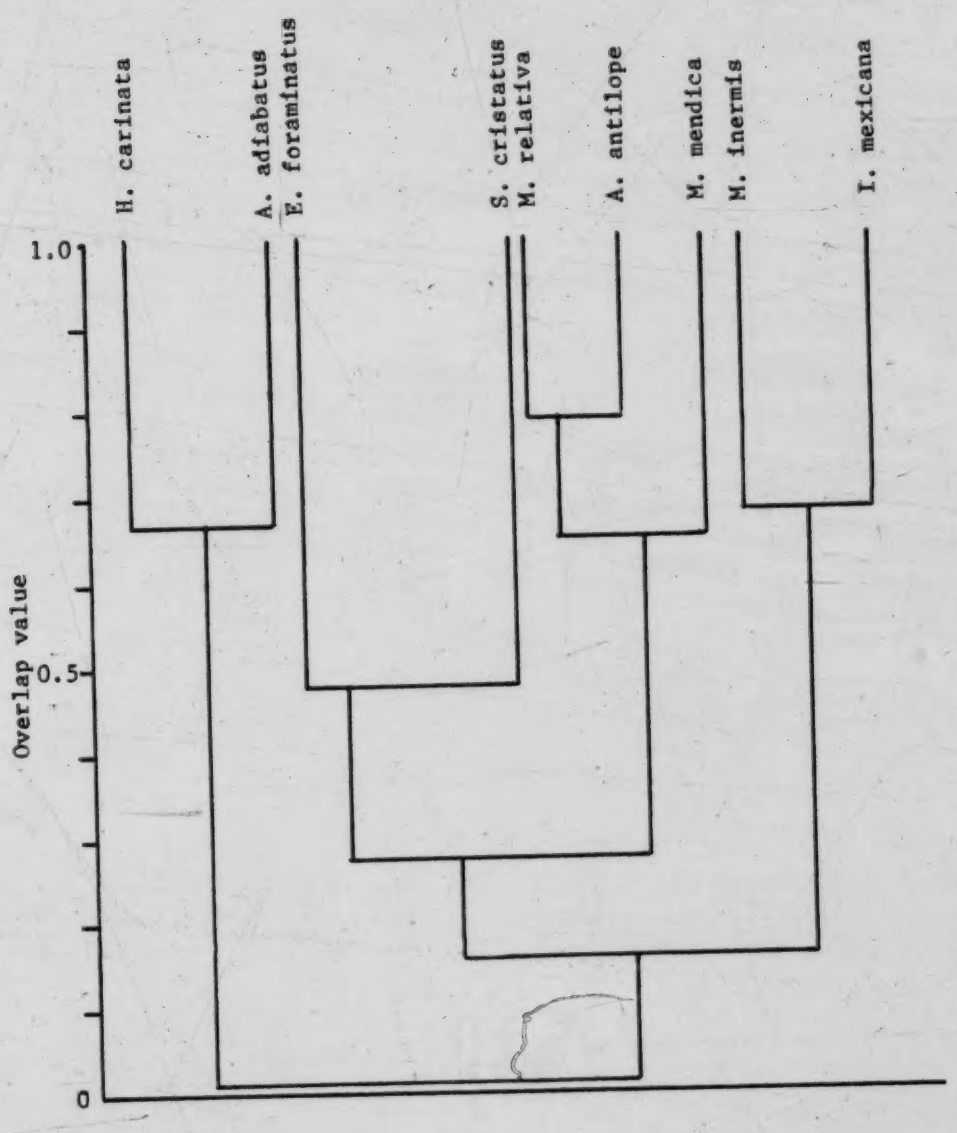

Figure 7 - Dendrogram showing grouping by overlap values for nest construction phenology of 9 species of charemophilous Hymenoptera from trap-nests at Lake Opinicon, Ontario.

6.5 Discussion

In temperate regions, climatic conditions place a severe restriction on flexibility of timing of nest construction for provisioning wasps and bees, particularly when such conditions affect blooming periods and prey availability. Nevertheless, different strategies of timing do appear to be present, both within bivoltine species associations, and between bivoltine and univoltine groups. Most of the apparently univoltine species appear at times when other groups occur in low densities, possibly reducing competition for holes. The benefits of such reduced competition may outweigh the benefits of increasing number of generations per year, even if this course were available. In a community in which the species have coevolved for some time, such selection pressures might produce a dispersion of phenology of nest construction. Here again, however, it is those species sharing a relatively similar nesting time which are particularly interesting. Such a group is that of A. antilope, M. relativa, and M. mendica. Avoidance of competition despite similar nesting times may be avoided by differences along other resource dimensions. Food type differences separate A. antilope from the others, although it is very similar in hole selection to M. mendica. The two leafcutter species may be separated on the basis of hole size selection, leaf type used for cell construction, and possibly pollen type as well.

In contrast, the difference between A. antilope and E. foraminatus is striking; while individuals of the two species prey on similar lepidopterous larvae, frequency peaks are different, and this is likely important to reduction of competition between the two.

In addition, Price (1974) suggests that where two or more generations are present for competing species, each generation may be exposed to rather different environmental conditions; one species may be favoured in one generation, and the other in another, and competition may never run to completion. Examining the data for these two eumenid species, it can be seen that E. foraminatus predominates in the first, or spring-early summer generation, while A. antilope occurs in much larger numbers in the latter generation.

Thus, by different times of appearance, and by differential investment in different generations, temporal partitioning is achieved among these species.

Chapter 7 - Larval Nutrition

7.1 Apoidea

Bees provide the young with plant material (pollen and nectar), whereas female wasps provide paralyzed arthropods to their developing larvae. This basic dichotomy between entomophagous and herbivorous groups means that there is no competition for food for larvae between the two. Adults of most Hymenoptera rely at least to some extent on nectar as a source of nutrition; however, for the purposes of provisioning the nest, it is only within each of the two groups that competition is important.

Detailed studies of the pollen were not carried out, and it is impossible to precisely determine the limits of type of provision. Preliminary examination of some nest contents does suggest that differences do occur, for example between H. carinata and M. relativa, where distinctly different pollen types were provided in at least some nests. Particularly when large numbers of bees are present, as they are here, this may be an important component of resource partitioning. Further study could be valuable in delimiting preference of different bee species. Iwata (1976) indicates that plants of the Leguminosae are the main sources of pollen for Megachilini, though he adds that this may only be due to the dominant position of that plant family, since no "special relationship" seems to exist.

Some studies have been carried out which indicate that indivi-

dual foraging females show a degree of preference for pollen type. Michener's (1954) work on M. brevis indicates that this species is rather restricted in its use of pollen sources, large families like Rosaceae being entirely unrepresented. Individual pollen constancy is noted as well, with pollen collecting females visiting numerous flowers of the same species during gathering of a single load.

It seems likely that the pollen selectivity may be an important source of differential resource use by leafcutter bees; this may be a function not only of flower abundance, but also of insect size, habitat, and other selective factors.

7.2 Entomophagous Wasps

The rest of the insects using the trap-nests are entomophagous, providing the larvae with a wide variety of arthropod prey. The factors affecting the general nature of prey use are probably largely historical, the limits defined by ancestral food selectivity.

7.2.1 Eumenidae

Most eumenid females provision the nest with hairless larvae of Lepidoptera; more rarely, some groups supply sawfly or beetle larvae to the young (Iwata, 1976). Females of the species present in the study site all stored Lepidoptera larvae with the exception of S. cristatus females which, like other members of that genus, stocked the nest with larval beetles. A brief review of prey records for various species is given below.

Ancistrocerus antilope

Females hunt caterpillars, like most of the other species.

Cooper (1953) studied hunting behaviour and states that they prey only on gelechioid and pyralid larvae, removing the prey from its leaf hideaway with the aid of the mandibles and stinging it into submission. Krombein (1967) found a much less restricted prey selection that included representatives of lepidopterous families Oecophoridae, Gelechiidae, Tortricidae, Phycitidae and Noctuidae; most cells contained a single species of caterpillar and 3-10 prey larvae per completed cell. Medler and Fye (1956) also found a wide prey selection. Individuals of Epipaschiidae, Gelechiidae, Phalaenidae, Phycitidae, and Tortricidae were all found to be used as nest provisions.

In the present study, prey records for five separate nests could be definitely attributed to this wasp. Representatives of three families of Lepidoptera occurred in different frequencies. Table 8 shows the cell examined, and the numbers of each prey type present. Tortricids are most frequently used, though this may be simply a function of the relative abundance of that group in a given area. Nest 78-5 makes it clear, however, that other families may be heavily preyed upon even when tortricids are available.

Euodynerus foraminatus

Krombein (1967) reported representatives of at least six families of Lepidoptera, including Gelechiidae, Tortricidae, Oecophoridae, Pyralidae, Epipaschiidae, and Pyraustidae. Medler (1964) reported all of the above except Epipaschiidae and additionally found representatives of Thyridae.

Prey specimens could only be associated with this species in

Table 8 - Prey records for *Ancistrocerus antilope* from trap-nests at Lake Opinicon, Ontario.

Nest/cell number	Prey family	Number examined (*) or total number in cell
29-4-2	Tortricidae	4*
35X-4-2	Tortricidae	5
	Olethreutidae	1
64-4A-2	Tortricidae	11
137-3	Tortricidae	1* (cell 1; 5 prey cell 2; 6 prey)
78-5-3	Drepanidae	7
	Tortricidae	1

two nests. In one, three pyralids were taken from the cell, and in the other a tortricid was used as prey.

Additional cell contents examined can be attributed to one or other of the above two species. These are listed below and indicate the generalized nature of provisioning by these wasps (Table 9). It seems most likely that both species discussed here have a relatively broad prey selectivity. As with many Hymenoptera, the initial cues may be related to habitat (Vinson, 1976); many representatives of the above lepidopterous families are leaf rollers, or miners, and Cooper (1953) discusses the hunting habits of females of A. antilope as they search appropriate plants and leaves. Possibly under conditions of extreme competition for food, a species such as E. foraminatus might specialize more highly on, for example, Pyralidae, although it is capable of a wider response and might thus respond in the presence of high prey densities or the absence of A. antilope. Additionally, size of prey varies within the hunting species, so this is not likely a factor in prey selection. These wasps will likely use as prey almost any individual of an appropriate family found in the hunting area.

Ancistrocerus adiabatus

The small wasps of this species are also caterpillar hunters, and Krombein (1967) has recorded prey individuals of Oecophoridae, Gelechiidae, Phaloniidae, Olethreutidae and Tortricidae in nests he examined. Previous works report similar groups used. Selection of smaller prey by females of this species may be a mechanism to partially avoid competition with the above species (A. antilope

Table 9 - Prey records for *Ancistrocerus antilope* or *Euodynerus foraminatus* from trap-nests at Lake Opinicon, Ontario.

Nest/cell number	Prey family	Number examined
5-4-1	Olethreutidae	3
17-4B-1	Tortricidae	5
	Pyralidae	1
18-2C	Pyralidae	1
23-3B-4	Tortricidae	1
43-3-2	Olethreutidae	2
	Gelechiidae	2
	Tortricidae	1
75-4A-3	Olethreutidae	17
	Tortricidae	1
134-4	Tortricidae	6
144-4	Tortricidae	6
148-4-3	Tortricidae	1

E. foraminatus) whose females use many of the same types of prey.

Symmorphus cristatus

As mentioned above, females of this behaviourally specialized genus hunt beetle larvae. Those nesting in the traps provisioned with chrysomelid larvae; the structural features of the caterpillars implied that the prey are external feeders, rather than leaf miners, making S. cristatus the likely predator, and verifying previous prey records for this species.

7.2.2 Sphecidae

Females of this family (sensu Bohart and Menke, 1976) provision with a wide variety of arthropods. Generally, more primitive members of the family prey on generalized arthropods, that is groups appearing earlier in geological time (Evans and Eberhard,1971). Of three species of sphecid using the trap-nests, two belong in the subfamily Larrinae and one in Sphecinae. These larrine species were formerly considered as only subgenerically different in the genus Trypoxylon, but are now recognixed as generically distinct.

Trypoxylon frigidum

Females of this species hunt spiders, preying largely on snare-builders, but occasionally taking wandering spiders. The large size difference between members of this species and those of Trypargilum striatum probably indicates the use of different sized prey. Females of T. frigidum appear to concentrate on theridiids (a family whose members are not used by Trypargilum striatum) and on araneids as well, often immatures (Krombein, 1967).

Trypargilum striatum

Krombein (1967) reports the principal prey of females of this species as araneid spiders, with a few thomisids and pisaurids, at a locality in New York State. This predominance of web-spinning spider prey appears indicative of hunting behaviour used; taking prey from webs rather than from the ground contrasts with the behaviour of females of other species in the same genus, as pointed out by Krombein.

Isodontia mexicana

Females are large and, unlike the groups discussed above, are highly specilaized hunters. Bohart and Menke (1976) indicate gryllids and tettigoniids (Orthoptera) as preferred prey of members of the genus as a whole, and this species is no exception. Medler (1965) records individuals of four genera of Tettigoniidae and five species from two genera of Oecanthinae (tree crickets) used as provisions for the larvae.

Prey samples were taken from six nests. Records are shown in Table 10. The distinctive dichotomy in prey choice seems to indicate an individual selection of one family of prey or the other. Nests contained either conocephaline grasshoppers or oecanthine crickets, but not both in one nest. Since the relative size of grasshopper nymphs is much less than that of tree crickets, it is not surprising to find much larger numbers of the former.

7.2.3 Pompilidae

Dipogon sayi

Medler and Koerber (1957) record prey of females of D. sayi as

Table 10 - Prey records for *Isodontia mexicana* from trap-nests at Lake Opinicon, Ontario.

Nest/cell number	Prey genus/species	Number in cell
41-4-1	*Oecanthus quadripunctatus*	cell 1; 10 prey
	O. nigricornis	
97-5A	*O. fultoni*	
109-4A-1	*O. quadripunctatus*	9-10
94-4-3	*Conocephalus* sp.	30
94-5A-1	*Conocephalus* sp.	14

belonging to four spider families, Amaurobiidae, Gnaphosidae, Salticidae, and Thomisidae, the majority in the last family, genus Xysticus. Each cell is stored with a single prey, and thus most prey are fairly large.

Prey taken from two pompilid nests proved to be individuals of Xysticus discursans (Thomisidae), a species not mentioned by the above authors, but within the expected range of prey choice. Krombein (1967) similarly found only Xysticus spp. to be used as prey.

7.3 Discussion

Preliminary investigation suggests differential pollen use by bees. The basic dichotomy of pollen feeding versus predatory habits negates the possibility of competition between bees and wasps for larval food.

Within entomophagous species associations, the situation varies widely. A species like S. cristatus, whose females use prey virtually untouched by other wasps, competes little for food with these groups. Similarly, females of the sphecid I. mexicana have their own special prey choice i.e. orthopterans. Both Trypargilum striatum and Trypoxylon frigidum females are spider hunters, but probably use different sizes of prey, and likely both use smaller prey than D. sayi females, since these last store only a single prey per cell. This pompilid preys on an entirely different group of spiders, taking mainly errant forms, rather than web-spinning types selected by the above sphecids.

Other eumenids present a more puzzling situation. All seem to prey on a wide variety of lepidopterous larvae, displaying extensive overlap between species. It would seem that there could be a great deal of competition for prey, although sufficiently large populations of lepidopterous larvae, in the right habitat, combined with a broad prey choice, could substantially reduce such competition.

Flexibility of prey selection is probably largely a function of historical factors. Characteristic host specificity of many solitary wasps (Evans, 1970), particularly in generalized groups, allows for a high degree of prey type partitioning within a given community. In fact, it is here that competition from ground nesting species may be most severe, since related ground nesters often take prey similar to that used by related charemophilous counterparts. This is likely so for sphecids and pompilids, and possibly bees in the area.

Eumenids are relative generalists in food type, selecting prey from a number of families, and undoubtedly being restricted more by prey habitat preference than by actual selection of individuals of a given family. Such a generalist strategy may allow sufficient flexibility in the face of strong potential competition to avoid actual problems with sufficient food resources. Evans (1970) wrote that "since the arthropods used as prey are generally those present in large numbers during the nesting season, and since each species is a specialist, it is not likely that food shortage is often a limiting factor in wasp abundance". This is so for sphecids, but eumenids have apparently relied on a broad spectrum of prey selectivity combined with high overall prey numbers, to achieve the

same result.

It is interesting to view this in light of the social vespids, with an even more general prey selection (true carnivores), feeding almost any material to the larvae after maceration. Perhaps the success of that group, and the relative abundance of most of the generalist eumenids encountered here, is in part attributable to generalized prey selection.

Chapter 8 - Offspring Sex Ratio

8.1 Introduction

The ability of Hymenoptera to control offspring sex ratio has played an important role in evolution of social behaviour (West Eberhard, 1975; Trivers and Hare, 1976; Hamilton, 1972). Sex determination based on haplodiploidy and optional insemination of eggs is thus of interest in solitary and sub-social groups as precursors to eusocial Hymenoptera. According to Hamilton (1972) solitary groups should display equal investment in males and females, unlike eusocial groups which show a bias to production of females. Trivers and Hare (1976) have argued that, in fact, this is so, and that the situation in eusocial species is largely based on the ability of a colony queen to suppress "selfish" laying behaviour in her offspring. These authors use data from Krombein's (1967) study to imply such a 1:1 ratio of investment in solitary Hymenoptera. However, a number of points in Trivers and Hare's paper have been criticized by Alexander and Sherman (1977), including data used by Trivers and Hare to argue their point with respect to solitary trap-nesting aculeates (charemophiles). Alexander and Sherman note that sex ratio in a nest is dependent on hole size in which that nest is constructed; since Krombein's (1967) data collection was not regulated with respect to hole size, it cannot be used for demonstrating valid sex ratios. Alexander and Sherman state that "overall investment patterns obviously depended on the proportions

of the nests of each size that Krombein put out, and the significance of the size range he used would vary among species of differing body sizes".

The present experimental design accounts for this problem; nests were offered in equal proportions, and for at least five species the entire range of nesting sizes acceptable are represented. Aculeates have been faced with a natural choice, and relative numbers of different hole sizes used should reflect a natural tendency of the animals, and thus normal sex ratios of offspring. Offering the entire range of sizes capable of being used is a factor which has often been overlooked, and earlier works may be based on faulty assumptions.

Alexander and Sherman (1977) further argue that the design of Krombein's (1967) experiment, and thus also the present data, may have an effect on sex bias. Citing unpublished data of Cowan on E. foraminatus, Alexander and Sherman state that females nesting in bundled traps tend to bias the sex ratio of their broods more towards males than females which nest in single traps, since in the former arrangement, offspring are more likely to compete for mates with unrelated individuals. Alexander and Sherman discuss various aspects of such local mate competition and its effect on sex ratio.

It is worthwhile, then, to examine the present data in light if such ideas, particularly with respect to hole size selection of various species, and relation to sex ratio.

8.2 Results

8.2.1 Assumptions for Estimating Cell Occupants

Sexes of individuals from nests were recorded for all reared specimens. For most nests, some cell occupants were indeterminable as to the sex of occupant. However, based on previous work, it is apparent that order of sexes in nests is usually precise. All nesting females examined here placed female cells closest to the blind end of the boring, and male cells toward the entrance. Only very rarely does this sequence change. Krombein (1967) suggests that there may be two causes of altered order of sexes:

1/ supersedure by another females who begins her own sequence

2/ failure of released sperm to penetrate and fertilize eggs, resulting in a male developing where a female was intended.

In the present study very few reversals occurred. For M. relativa, only 3 of 91 nests (3.3%) showed this. Similar figures for other species are as follows: M. mendica 1 of 28 (3.6%); E. foraminatus, 1 of 63 (1.6%); S. cristatus, 0 of 13 (0%); A. adiabatus, 1 of 10 (10%); M. inermis, 0 of 10 (0%); A. antilope, 0 of 69 (0%). Assuming that sexes will occur in such an order, it is possible to estimate the sex of a given cell occupant for some cells. Table 11 gives sex ratios in different hole sizes for some species, and percent females.

8.2.2 Hole Size Effect

Data show clearly an effect of nest diameter, as has been shown and commented on by a number of authors (Cooper, 1953;

Table 11 - Sex ratio of cell occupants of 7 species of charemophilous Hymenoptera from trap-nests with holes of five different diameters at Lake Opinicon, Ontario (ratio is given as a function of the number of females, in the top half of the table, except where none of a given sex were produced, in which case absolute results are given; the bottom half of the table shows percent females in each hole size).

Taxon	Hole diameter (mm)					
	3	5	7	9	11	Overall
A. antilope	-	11:0	2.04:1	0.29:1	0.10:1	0.76:1
E. foraminatus	-	4:1	0.93:1	0.96:1	0.33:1	1.10:1
A. adiabatus	1.33:1	0.15:1	-	-	-	0.38:1
S. cristatus	-	5.67:1	4.67:1	0:3	-	3.44:1
M. relativa	-	40:1	0.66:1	1.24:1	1:1	0.95:1
M. mendica	-	1:0	1.79:1	0.84:1	1.25:1	1.44:1
M. inermis	-	-	-	7.50:1	1.20:1	3.00:1
A. antilope	-	0	32.9	77.6	91.3	56.8
E. foraminatus	-	20.0	51.8	50.9	75.0	47.6
A. adiabatus	42.9	86.7	-	-	-	72.7
S. cristatus	-	15.0	17.7	100.0	-	22.5
M. relativa	-	2.4	60.3	44.8	50.0	51.4
M. mendica	-	0	35.8	54.2	44.4	40.9
M. inermis	-	-	-	11.8	45.5	25.0

Stephen and Osgood, 1965; Krombein, 1967; Medler, see above), and as might be expected by differential cell volumes for males and females in Eumenidae. However, the effect is not as pronounced for some groups as for others. For all eumenids, percentage females and hole diameter are positively related; all three megachilid species, however, show a much less well defined relationship. Krombein (1967) has shown that for at least one of these species, M. mendica, there is no significant difference between lengths of male and female cells, unlike nests of eumenid species he has examined. This could account for dissimilarities between effects of nest diameter. Stephen and Osgood (1965) found a pronounced diameter effect in M. rotundata (=pacifica), and also noted that with increasing diameter of nest, sex ratio approached 1:1.

It is not entirely clear what mechanism a given female uses to determine whether a cell will be male or female producing. Evans' (1970) comment that depth of the ovipositing female within the burrow is a determining factor is puzzling, and at any rate an oversimplification, though this may be a factor.

Overall sex ratios for species examined show wide variability even within a given family. Thus while A. antilope, E. foraminatus, and M. relativa show a ratio close to 1:1, M. mendica produces a slightly male biased sex ratio, and both S. cristatus and A. adiabatus show strongly biased ratios, the former toward males, the latter toward females. Similarly, Stephen and Osgood (1965) found a male bias in M. rotundata (=pacifica). The figures for M. inermis, while showing a male bias, are possibly dubious, since the entire

range of acceptable hole diameters was not available. However, the above authors mention studies with similar findings for this species.

Such overall ratios should reflect a natural situation as described previously. In some comparisons a smaller sample size may affect these figures, but even estimated ratios show a similar or greater bias. Comparison with Trivers and Hare's (1976) data show some striking differences. In virtually all of their figures, using Krombein's (1967) data, ratios are strongly male biased; this is contrary to my observations. Krombein's traps were mostly 4.8 mm or 6.4 mm in diameter, a range which would inadequately cover nest size selection in almost all of the more abundant species encountered. It is notable that for A. adiabatus, nesting in small holes with an adequate range covered in Krombein's study, the ratio is very similar to that found in the present study.

These results clearly show, as suggested by Alexander and Sherman (1977), that it is inappropriate to use Krombein's (1967) data to discuss the outcome of parent- offspring conflict as supported by 1:1 investment ratios in solitary aculeates. Relationship between mean of frequency distribution of hole size selection, and changing sex ratio with hole diameter, will be discussed below.

8.2.3 Generation Effect

The presence of two generations in some species, and the ability to alter sex ratios of offspring allows an examination of differential sex ratio with generation. Table 12 shows relative numbers of males and females per generation for five species of bivoltine wasps and bees. Of these, three show a greater difference

Table 12 - Number and percentage of male and female cells in 5 species of bivoltine charemophilous Hymenoptera from trap-nests at Lake Opinicon, Ontario.

Taxon	Generation	Number of males (%)	Number of females (%)	Number of nests	
Ancistrocerus antilope	Summer	7(9.1)	69(90.9)	28	
	Overwinter	72(67.3)	35(32.7)	38	**
Euodynerus foraminatus	Summer	66(49.6)	67(50.4)	37	
	Overwinter	33(58.9)	23(41.1)	25	
Megachile relativa	Summer	37(32.2)	78(67.8)	24	
	Overwinter	180(54.4)	151(45.6)	64	**
Megachile mendica	Summer	23(69.7)	10(30.3)	8	
	Overwinter	41(54.0)	35(46.0)	19	
Megachile inermis	Summer	1(16.7)	5(83.3)	2	
	Overwinter	15(88.2)	2(11.8)	8	*

*,** - probability of difference between relative numbers of males and females in different generations greater than
* - .01
** - .005
Tested using 2 X 2 contingency test and the G-statistic.

between generations than might be expected by chance. Predictions for one of these, M. inermis, are based on a relatively small sample size, and as mentioned above, incomplete coverage of accepted hole sizes, possibly resulting in an artificial bias. The other two species, M. relativa and A. antilope, display a strong generation effect, both showing a female bias in summer generations, and male bias in overwintering, early summer emerging generations. M. inermis also shows this effect, though to a lesser extent.

Such a tendency may be involved with the expendibility of males, the smaller investment of energy in provisioning for them (fewer prey, less pollen), and the mortality in overwintering wasps and bees. Males emerge first, and a larger number of males dispersing from emergence sites may increase the probability of females being inseminated, and guarantee a larger percentage of successful females, though actual numbers may be small. Both M. relativa and A. antilope reach peaks of nesting abundance at the end of the nesting season; selection has resulted in such a pattern and relative numbers of males are greater during that period subject to greater mortality (i.e. winter climatic extremes). The timing of such peaks of frequency may be tied to sex ratios in different generations.

Chapter 9 - Discussion

Insect communities provide useful opportunities for examination of some aspects of theoretical ecology, since many are composed of divergent elements exploiting a vast array of resource states, and yet include associations of species which are ecologically similar. Evans (1970, 1973) has studied the wasp fauna of Jackson Hole, Wyoming comparing both ground nesting and aerial hole nesting solitary species with respect to a number of resource dimensions, notably nesting sites and food relationships. Complex interactions discussed in ground nesters in the earlier study imply that a similar examination of charemophiles would add much to observational studies already carried out.

In such a community, two resources are notable, mainly nesting sites, and food. Necessity for reduction of competition results in a number of changes in species composing a community over time, such that differences may appear in patterns of resource use (different hole sizes, different food types) or by temporal distinctions between similar patterns, or combinations of the above.

Examination of hole size selection and temporal distribution, and to a lesser extent, trophic partitioning, reveals an unclear picture of reduced competition due to differential resource use. Both the former dimensions show certain elements relatively separate from the rest of the species; however, and perhaps more interestingly, all dimensions include groups of very closely associated species,

which overlap considerably. The largest part of such groups do not display a noticeable inverse overlap relationship from dimension to dimension, as might be expected if the dimensions were essentially independent (Schoener, 1974). Thus, M. relativa, M. mendica, and A. antilope are grouped according to both hole size and seasonal distribution. Rather than displaying a major degree of partitioning along a single dimension, these similar species show minor differences in two dimensions which, when combined in an analysis of the realized niche, provide sufficient ecological distance to allow coexistence at relatively high densities.

To examine more closely the overall niche differences of species involved, a product overlap matrix has been produced (Table 13) by multiplication of the overlaps on each of the measured dimensions, and a dendrogram calculated and drawn from it (Figure 8). Similarities between this dendrogram and those for hole size selection and nest construction phenology are quite striking, reinforcing absence of an inverse relationship between overlap on different dimensions. Two isolated groups, consisting of small hole users with a single frequency peak, and central date abundance on the one hand, and of large hole users with a later appearance occur in all three figures. Similarly, the three species M. relativa, M. mendica, and A. antilope show close associations in both dimensions examined quantitatively. Most significant is the discrepancy between the relationship of E. foraminatus with other species. While hole size associates it with the three above mentioned species, it differs in seasonal distribution, and is more closely associated with the

Table 13 - Product overlap matrix of nest diameter selection by nest construction phenology for 9 species of charemophilous Hymenoptera in trap-nests at Lake Opinicon, Ontario.

Taxon	Taxon								
	1	2	3	4	5	6	7	8	9
1. *A. antilope*	1.0	.53	.39	.60	.79	.03	.32	.06	.06
2. *E. foraminatus*		1.0	.12	.44	.49	.04	.17	.11	.48
3. *I. mexicana*			1.0	.29	.21	.005	.68	.003	.005
4. *M. mendica*				1.0	.70	.002	.12	.006	.02
5. *M. relativa*					1.0	.02	.12	.03	.12
6. *H. carinata*						1.0	0	.66	.005
7. *M. inermis*							1.0	0	.003
8. *A. adiabatus*								1.0	.008
9. *S. cristatus*									1.0
Mean overlap	.35	.30	.21	.27	.31	.10	.18	.11	.09

Grand mean = .21

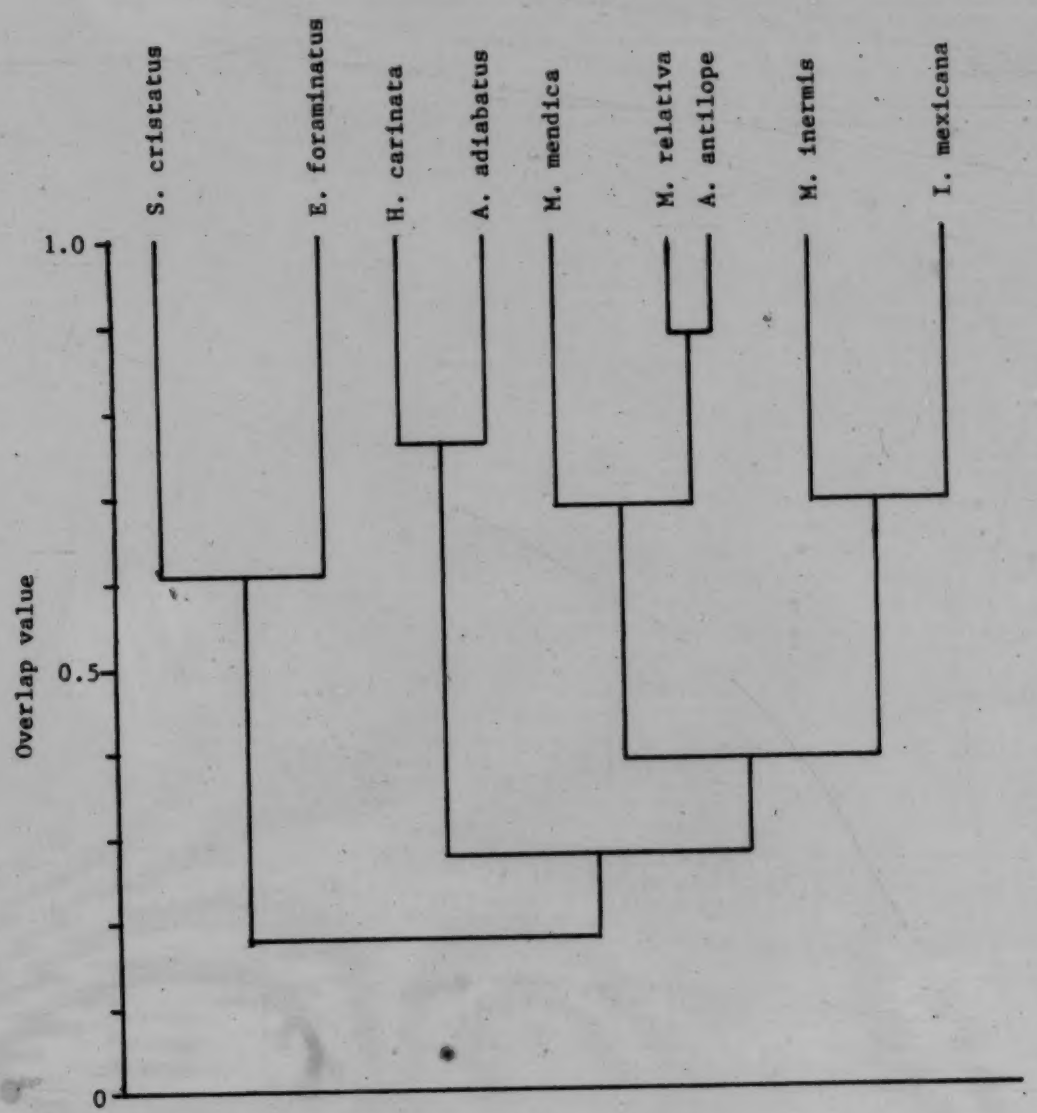

Figure 8 - Dendrogram showing grouping by product overlap values of hole size selection and nest construction phenology for 9 species of charemophilous Hymenoptera from trap-nests at Lake Opinicon, Ontario.

rather isolated S. cristatus.

Overall associations, however, still relate E. foraminatus to A. antilope, M. mendica and M. relativa on the basis of high overlap values between these species for hole size selection. Such overlap raises the question of whether or not this is due to nest site availability not being a limiting factor. In view of extremely high use of artificial traps, it seems unlikely that sufficient numbers of natural nesting sites are available. McNaughton and Wolf (1970) argue that the concept of limiting factors has been overemphasized, and that some competition may be considered to occur between individuals using the same resource, regardless of the availability of that resource. At any rate, apparently differences in timing of nesting are sufficient to avoid overt competition for nest holes, or at least prevent such competition from running to completion with total exclusion. Another possibility has been suggested by Koerber and Medler (1958) who feel that A. antilope and E. foraminatus differ some in habitat preference, the former occurring in more heavily wooded locations, the latter in more open areas. Such differences, related to surrounding vegetation density, may be a part of resource partitioning for some species in the association. If so, these two species may, for example, use available habitat at different stages of succession, one nesting in early stages of field succession, the other in more heavily overgrown areas. In the present study, it is impossible to determine strict differences in habitat type which clearly separate these two species. This does not refute the idea that differential habitat selection may exist, only that they cannot

be distinguished here.

The restricted area examined in this study, and appearance of both species at almost all trap locations shows that even if such a tendency is present, nesting site selection is not mutually exclusive. Precise trap positioning, and observation of behaviour of individuals would allow a more definitive statement on such factors.

Perhaps the most noticeable trend here is that those species displaying relative generalist approaches (i.e. broad niched) are the most abundant species in the community. This would imply that despite high overlaps between such species in a dimension such as hole size, other factors are involved which significantly reduce the potentially negative effects of competition. Thus, in comparing groups such as E. foraminatus and A. antilope, which overlap considerably in hole size selection and food type, seasonal differences occur whereby nest site searching and prey hunting are at their peak for each species at somewhat different times. Similarly, the relative investment of each species in two annual generations may differ sufficiently that competition is not sufficiently intense in one generation to have detrimental effects.

While M. mendica and M. relativa also overlap considerably in hole size selection, the relatively unrelated species, A. antilope, is more similar to M. mendica with respect to phenology, reducing food type competition. This gives the general effect that pairs of disparate species are most similar on an overall basis throughout this association of species. A large leafcutter, M. inermis and the sphecid, I. mexicana; a small leafcutter, H. carinata and A. adiabatus;

M. relativa and A. antilope; and M. mendica and E. foraminatus are most closely associated species pairs.

S. cristatus is unusual in both hole size selection and seasonal distribution. Particularly in food type, it is relatively ecologically isolated from the rest of the guild, in what would appear as an ideal enclave for niche expansion, and population increase, and yet absolute numbers of individuals remain low. This implies that the niche of this species is restricted either by intrinsic factors, or by competitors outside the guild, rather than by pressure from competing species within this association of charemophiles.

Most relative specialists are uncommon. Populations are small compared to the five most abundant species, the exception being I. mexicana which overlaps less with this major group and is still relatively common, perhaps because it differs in almost all dimensions examined.

It appears that a generalist strategy, particularly with respect to hole size and prey type, allows certain species to increase in numbers despite high levels of potential competition. A broad range of acceptable resource states makes it possible for a species to use resources which are less heavily used by other groups. Thus, eumenids preying on lepidopterous larvae are able to take virtually any insect encountered in the right habitat (leaf rollers), and take advantage of high overall population levels, even if one specific prey type is not numerous. This would provide for a shift in selection by a species in the face of heavy competition.

The data here agrees with Pianka's (1974) comments on specialists

and generalists. He states that, "Highly specialized organisms ... usually, though not always, have narrow tolerance limits along one or more of their niche dimensions. Often such specialists have very specific habitat requirements, and as a result they may not be very abundant. In contrast, organisms with broad tolerances are typically more generalized, with more generalized habitat requirements, and are usually much more common. In other words, specialists are often rare, while generalists are more abundant".

Note, too, that females of a specialist such as S. cristatus, using hole sizes frequently occupied by other species, tend to appear much earlier than most of the latter. If S. cristatus females are restricted in hole selection, early appearance would provide a distinct advantage in finding such holes, when populations of most competitors are still low. Females of a generalist, on the other hand, less strongly affected by a "loss" in a scramble competition, will be capable of selecting other suitable holes.

Sex ratios of eumenids can differ drastically with hole diameter. What is the relationship between selected hole size and resulting sex ratio? If a 1:1 ratio is expected in solitary bees and wasps (Hamilton, 1972) then it would seem probable that the mean of the frequency distribution for hole size use should correspond to such a ratio. This, in fact, is so for four of the six species for which sex ratio data have been examined. E. foraminatus and A. antilope show an extrapolated 52% female bias, while M. mendica and M. relativa are close to this as well. Individuals of these two families achieve this in different ways; megachilids show fairly stable ratios above

a certain diameter of nest. In contrast, eumenids with differences in sex ratio dependent on nest hole diameter, balance sex ratio by the distribution of hole sizes used.

Two species are divergent from the above pattern. S. cristatus shows a strong male bias at the mean hole diameter used, and A. adiabatus shows a strong female bias, like the bivoltine species; S. cristatus produces a single overwintering generation, and like M. relativa and A. antilope, is male biased, while A. adiabatus with its summer generation shows a female bias.

Apparently a conflict must be resolved among aculeates using a range of hole sizes; if 1:1 sex ratios are optimal, range of hole sizes to be used is restricted unless a certain diversity of sizes are available. It would seem more adaptive to select a variety of hole sizes, and manipulate sex ratios therein, than to attempt to discover an ideal hole size for production of equal numbers of males and females, resulting in excessive use of energy for minimal gain. This may explain the abundance of nest diameter generalists.

Association of species in a community has long been recognized to follow a pattern including both rare and abundant species. That almost all abundant species examined in this study are generalists implies ability to use a diversity of resource states, and thus reduce potential competition. This allows an increase in numbers rarely achieved by overall specialists which may be limited by availability of required resource states.

Fluctuations in populations from year to year as documented by Krombein (1967) may be related to availability of specific

hole sizes, and coincident increase of species rare in other years, which could reduce overall abundance of generalists as well. The abundant nature of several of the species studied implies, though does not prove, the dominant nature of those species within the guild. Both McNaughton and Wolf (1970) and Price (1971) have discussed the idea of dominance with respect to the niche in communities. Price lists several factors which permit high relative abundances, including discovery of a new, unused resource, specialization for adaptive superiority over a portion of a resource which is widely distributed, or exploitation of a broad spectrum of resources by a generally adapted species. The latter results in occupancy of potential niche space of other animals.

Here again, examination of the nature of the niche of a species in the absence of ecologically similar species will give information on whether a species is really dominant over another.

In light of Price's (1971) comments on dominance of a single parasitoid species on the basis of competitive ability, it is more difficult to understand the large number of relatively abundant and possibly dominant species unless the amount of generalization allows less efficient but generalized species to fit along the resource gradient. The relationship between M. relativa and M. mendica would be particularly interesting in this respect if more closely examined.

Price's (1971) model relating abundance to genetic diversity, and thus a broad realized niche, may apply to the present study. Species associations such as that examined here, will allow inter-

community comparisons, and further elucidation of broader principles of community diversity. Only by use of quantitative analyses, however, can such comparisons be made.

Chapter 10 - Concluding Remarks

The present study can only be a preliminary investigation of trends in such an association of these species. Niche breadth and overlap measures of members of a single guild, or community, are limited in the phenomena they can describe. With such a baseline, however, and with the relationships examined for a given group such as the charemophilous Hymenoptera, it then becomes possible to suggest ways in which these data can be expanded upon and reinterpreted in light of further work.

Initially, it is important to examine similar associations to determine if the niche of a given species is relatively constant in the face of differential pressures from climate, competitors, and the like. Krombein's (1967) work has shown that in other localities such hymenopterous guilds may be more, or less, diverse, with varying associations of species. McNaughton and Wolf, (1970) discuss how a new species may affect the niches of established species, assuming a close approach to saturation of the available resources. They state that species may join a system either at a rate equal to increase in carrying capacity, resulting in stable niche breadths despite changing diversity, or they may be added more rapidly, resulting in compression of niches. This fails to account for the assumption that where system saturation is not complete, a generalist may enter by exploiting inefficiently used resources.

Studies of more, or less diverse communities will determine

stability of the niche of a species under differing conditions, and allow further conclusions concerning form of species packing and new additions.

Examining the nature of a species' niche in different parts of the geographical range and over different periods (e.g. years) allows determination of species variation as well. The area examined in the present study may, for a number of species present, be a limit of the normal range. Does this place such species at a competitive disadvantage, where they must generalize or specialize more than in other parts of the range to successfully compete with better adapted groups? Multivoltine animals may be more severely selected against under conditions of greater climatic selective pressures (i.e. with increasing latitude or altitude) whereas a univoltine species may be more precisely coordinated with environmental extremes. Studies from various geographical locations will give some idea of whether such effects are more important than solely presence or absence of certain competing species.

Examinations of populations in communities over time periods of years will additionally determine if the nature of the niche is constant, or if breadth and overlap are determined by other selective pressures. These studies, and those mentioned above will test practically May and MacArthur's (1972) theoretical model stating that the limit of niche overlap is insensitive to degree of environmental fluctuation, unless severe.

It is the comparative examination of community and guild relationships, made possible by the use of quantitative niche measures,

which will allow a greater understanding of interactions between associations of similar species. While the present study indicates certain trends in such associations, and the importance of abundance, dominance, and specialization/generalization, it will be most important as a starting point for additional work on similar groups, and the nature of intercommunity comparisons.

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AUTOBIOGRAPHY

I was born on May 23, 1954 in Ottawa, Ontario, where I completed my primary and secondary schooling. While fascinated by animals from an early age, and with few serious doubts as to what I would do when (if?) I grew up, insects were not an all consuming interest, and I lacked the collecting and pinning instinct common to many who go on in entomology. Nevertheless, biology was the most important thing, and the house was frequently populated by diverse fauna, from newts and snakes to white rats.

From 1971 - 1975 I attended Queen's University in Kingston, Ontario in a B.Sc. programme in biology, and while there began to focus my attention on insects and entomology thanks primarily to Dr. A.S. West, whose humour and habit of locking doors as soon as a class started made attendance at 8:30 a.m. worthwhile. Extra impetus for these interests was provided when I worked in the Hymenoptera section of the Biosystematics Research Institute in Ottawa for the summers of 1974 and 1975.

Having completed my undergraduate degree, I arrived in Edmonton in September, 1975 to start work on a masters programme.